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Distributional and Dimensional Patterns of Muskrat Burrows

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DISTRIBUTIONAL AND DIMENSIONAL PATTERNS OF MUSKRAT BURROWS

by

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ABSTRACT

The dimensional, distributional and occupancy patterns of muskrat (*Ondatra zibethicus zibethicus*) burrows were studied from 1 September 1976 to 13 November 1977 in 3 study areas located in Branched Oak Lake, a 2,238 ha recreation area in southeastern Nebraska. A seasonal shift from burrows to marsh lodges was detected within the resident population of muskrats. Information gathered from changing patterns of predation and in field muskrat carcass examination suggested the occurrence of Errington's or Tizzer's disease. The dimensional and distributional characteristics of burrows were described by a list of internal, external, physiographic and edaphic variables. This list of 54 descriptive variables was condensed, in a stepwise fashion, through the use of SAS 76 programs MEANS, CORR, FREQ, and SCATTER. A final list containing 8 significantly correlated internal and external variables was used in the CLUSTER program to segregate 85 muskrat burrows into 9 burrow types. The most complex burrows were located within areas of loam substrate of less than 30 degree slopes characterized by homogeneous plant communities. The only evidence of reproduction in the 3 study areas took place within these complex burrows. The least complex burrows were located in physiographically and edaphically diverse areas characterized by heterogeneous plant communities. A system, using the detectable defining variables of the 9 burrow types, was proposed for the qualification of substrate suitability as burrowing material and for the enumeration of resident burrowing muskrats.

INTRODUCTION

The objective of this study was to provide baseline data for an area-specific census method for bank burrowing muskrats (*Ondatra zibethicus zibethicus*).

Muskrat population estimates presently are primarily concerned with lodge counts in large marshes. Where both burrowing and lodge dwelling muskrats are present, this procedure is inaccurate.

Census methods using lodge counts have been outlined by Lay (1945) and Dozier (1948). Although the methodology varies slightly from region to region, the lodge count has been accepted as a useful and widely applicable management tool.

In areas in which the resident muskrat population dwells in both burrows and lodges, there are generally 3 types of occupancy patterns. One segment of the population dwells in burrows, the second lives in lodges and the third alternates between burrows and lodges. There is some evidence indicating that this last segment may prefer lodges during the fall and winter and burrows during the rest of the year (MacArthur and Aleksiuk 1979). Because of variable dwelling behavior, only counts during the fall and winter are approximately accurate.

If one accepts Errington's (1940) and Ognev's (1948) contention that burrows are the "ultimate refuge" of muskrats then it is reasonable to assume most managers would recognize the necessity of developing a census method for burrowing muskrats. The only methods presently available are the burrow breeding territory count (Errington 1943) and estimates based on the ratio of bank burrowing muskrats to lodge dwelling muskrats (Lay 1945). Both Errington's and Lay's methods require either an intimate knowledge of muskrat habits and habitat or long term harvest information.

A limited number of studies have described the structure and/or distribution of muskrat burrows (Beshears and Haugen 1953, Earhart 1969). Earhart described the distribution, structure, function and occupancy of burrows by muskrats in California farm ponds.

OBJECTIVES

This study was undertaken to satisfy the following objectives;

(1) Determine use of loam, clay and sand substrates by burrowing muskrats.

(2) Separate burrows into types based on the quantifiable, dimensional and distributional, internal and external burrow characteristics, and external parameters of the environment.

(3) Determine the length of occupancy and category of usage of each burrow type.

(4) Formulate a census method for bank burrowing muskrats using occupancy patterns and external characteristics of burrow types.

LITERATURE REVIEW

Muskrats inhabit many still and flowing water habitats throughout most of North America and much of central and northern Eurasia (Errington 1963). This prolific semi-aquatic rodent is considered economically valuable throughout its native range and in the northern part of its adopted range in Eurasia. In many instances harvests of muskrats exceeds that of all other harvested furbearers in number and in value (Geller and Skrobov 1967). The burrowing habits of muskrats have necessitated extensive control programs in some parts of their adopted range (Warwick 1936, Van Troostwijk 1976).

Most management programs, both control and enhancement, are concerned with detection and enumeration of muskrats. The methods vary but all rely on the recognition of the structures built by the muskrat.

Marsh Structures

Authors working in the northern half of the muskrat's range (Johnson 1925, Sather 1958, Davydov 1968) described 4 types of structures utilized by marsh dwelling muskrats. These structures differ in construction, function, distribution and longevity.

The dwelling lodge is roughly hemispherical and usually constructed of a mixture of surrounding vegetation interspersed with mud. Although generally dome-like, it may assume many configurations ranging from flattened ovals (Dozier 1948) to nest-like structures in trees. The structures vary in all dimensions. They usually extend 0.3 to 1.3 m above water and may have a total height of 0.5 to 1.5 m. The typical dwelling lodge is 1.5 to 2 m in diameter (Johnson 1925), but may reach

8 m (Dozier 1948).

Most dwelling lodges have a single, irregular, above water chamber with 2 or more exits or plunge holes leading to below water exits. During drought these plunge holes will lead to tunnels in the substrate that eventually end at deep water openings. Irregular shaped lodges frequently have 2 or more internal chambers on various levels with small pocket-like chambers in the exterior walls (Earhart 1969, Errington 1963). Seasonal modifications in the number and location of these internal chambers in response to changing temperature were described by MacArthur and Aleksiuk (1979).

The second structure or feeding house is smaller than dwelling lodges and normally rises no more than 0.6 m above the water (Sather 1958). These small mounds of aquatic vegetation are less regular than dwelling lodges and most frequently contain a single central chamber with 1 plunge hole exiting under water.

The third structure or pushup occurs only in marshes covered by ice. These very simple structures are constructed above a hole in the ice. They are made from wadded vegetation and mud pushed through the hole by muskrats. As this material accumulates and freezes, the muskrat excavates a small internal chamber (Davydov 1968). These misshapen mounds of vegetation are usually no more than 0.5 m tall.

The fourth structure, or feeding platform, is a raft-like construction that ranges from barely floating accumulations of food scraps 0.5 m in diameter, to solid, anchored, flat-topped mounds 1.5 m in diameter (Lay 1945, Willner et al. 1975).

Chambers within lodges, in their simplest form, are 25 to 40 cm long, 20 to 25 cm wide and 15 to 20 cm high. This chamber size is frequently occupied by a single muskrat. As the number of occupants increases, length and width dimensions increases as well as the irregularity of the chamber outline (Johnson 1925).

Stability and duration of the dwelling lodge, feeding house and feeding platform are entirely dependent on water level fluctuations and amount of wave action (Lay 1945, Sather 1958, Danell 1978a). Lodges securely anchored in inundated trees or shrubs may survive the average spring high water level but those structures not so located soon disintegrate, especially when seasonal high water is combined with strong wind (Bellrose and Low 1943).

Typical marsh dwelling lodges and feeding lodges are located in water from 30 to 120 cm deep (Aldous 1947, Sather 1958). Those located at either end of this range are considered marginally situated.

Those lodges located in water deeper than 1.2 m are frequently at or beyond the boundary of emergent aquatic plant growth (Errington 1948). Without the break-water protection afforded by emergents, high wave action soon outpaces repair efforts by the residents. Adaptations to this condition are lodges located on localized high spots in the substrate, logs and root clumps (Neal 1977, Danell 1978a). The security afforded by these features is evidently enough to counter balance seasonal high wave action.

Lodges located in water less than 50 cm are subject to freeze out in winter. This typically occurs when ice freezes to the bottom. They are also subject to exposure during drought. Under either circumstance the typical adaptation is to plug the blocked or exposed openings, redig the plunge hole to a point below the frozen or exposed portion of the substrate and then excavate a horizontal tunnel to useable water (Johnson 1925, Errington 1939).

Distribution and number of feeding lodges, pushups and feeding platforms depend on the distribution of dwelling lodges. The reported ranges vary from 1 feeding structure to 2 dwelling lodges (Bellrose 1950) to 2.69 feeding structures per dwelling lodge (Dozier 1948). Davydov (1968) suggested that the ratio of feeding structures per family unit is a direct measure of family size and quantity, quality and distribution of food.

At the end of the breeding season it is generally considered that one family unit composed of an adult female, her last litter and an occasional adult male occupy each dwelling lodge (Dozier 1948, Sather 1958, MacArthur 1978). MacArthur further suggested there was no logical reason to assume only 1 family unit per dwelling lodge before the breeding season.

Burrows

Most descriptive studies of muskrats described some physical aspect of burrows. Beshears and Haugen (1953), Earhart (1969), Danell (1978b) and Chulick (1979) have completed comprehensive studies on burrows or burrow distribution.

Dimensions of burrows in Alabama farm ponds were described by Beshears and Haugen (1953). Although no separation into types was attempted, mention of differential use suggested several types were examined.

Durability, occupancy and substrate soil texture of burrows in California farm ponds was analyzed by Earhart (1969). Earhart described 3 distinct burrow types using an extensive series of environmental and dimensional variables. Seasonal changes in occupancy patterns were determined through kill-trapping burrow residents. Temperature differences within burrow types located in different substrates were examined. Territorial interactions were described on the basis of occupancy patterns and kill-trapping information.

Van Troostwijk (1976) reported width (1-2 m) and bank penetration (1-4 m, maximum = 20 m) of burrow systems and maximum depth of burrow openings below water (1.7 m) in dikes and poulders in the Netherlands. A characteristic opening width of 100 to 115 mm and maximum opening depth below water of 0.9 to 2 m was found for muskrat burrows that formerly existed in English waterways (Warwick 1936). Warwick determined that the opening widths increased over time through use by muskrats and wave action. Errington (1937a) stated that burrow openings of complex systems may be 0.6 m or more above water level. The most extensive system so far discovered in the literature was described by Carter (1922). This system had a main tunnel chamber approximately 60 cm in diameter lined with soft, dry grass. The main tunnel had 4 side tunnels, filled with foodstuffs, that had a combined length of 14.6 m. This structure was excavated by muskrats in less than 2 months.

Distributional patterns of burrows and lodges in Sweden, with respect to water depth, distribution of vegetation, soil particle size and effects of territoriality were described by Danell (1978b). Effects of habitat quality, measured by vegetational distribution, soil, bank and stream characteristics, were measured for a stream dwelling population of burrowing muskrats in Pennsylvania by Chulick (1979).

Existence of differentially used muskrat burrows was described by other authors. Both Johnson (1925) and Errington (1948) described burrows that were transitory (feeding) or continuous (breeding). Small dens or feeding burrows were considered accessory structures to more complex systems and served as refuges near concentrations of food. As the muskrat population increased, these burrows were occupied and enlarged by young of the year (Shanks and Arthur 1952).

Errington (1937a, 1939, 1940) stated that complex burrows served both as the loci of activity and as the last stand of environmentally stressed burrow-dwelling muskrats. The idea that these extremely complex burrow systems served as the "ultimate refuge" also was proposed by Dozier (1948), Ognev (1948) and Danell (1978b).

Johnson (1925) and Errington (1963) recognized an aggregated spacial pattern of muskrat burrows. This aggregated pattern indicated a social organization of small family groups in rodents (Stromberg 1978).

Distribution of burrows was dependent upon substrate soil texture, reinforcing root systems, slope, distribution of emergent aquatic plants and stability of water levels (Errington 1948, Earhart 1969, Danell 1978b, Wilson and Killgore 1978). Reported burrow densities ranged from 6.59 and 11.54 per 100 m of stream bank in Pennsylvania (Chulick 1979) to 0.47 burrows per 100 m of bank in a shallow Swedish lake (Danell 1978b). Iowa densities of bank burrow breeding territories ranged from 3.6 per 100 m in high quality habitat to 0.2 per 100 m in low quality habitat (Errington 1940).

Occupancy patterns among burrowing rodents were influenced by age of occupants, social pressure, seasonal abundance and distribution of food material (Yahner 1978). Those factors of generalized rodent burrow spacing were analogous to the attachment to old complex burrows by dominant agressive muskrats (Errington 1937a, 1939), the settling of peripheral burrows and territories by juveniles (Errington 1940) and construction and utilization of new feeding burrows adjacent to seasonally abundant stands of emergent aquatic plants.

The reported number of occupants per burrow ranged from 1.2 per burrow in poulder banks and 4.1 per burrow in canal banks in the Netherlands (Van Troostwijk 1976) to 30 muskrats in a single burrow in Maryland during winter (Bailey 1937).

Characteristics of soil affecting burrow distribution included particle size (Earhart 1969, Danell 1978b, Chulick 1979), fertility (Chulick 1979), porosity (Wilson and Killgore 1978) and moisture content (Ognev 1948, Walker 1975, Kay and Whitford 1978). The effect of particle size upon distribution of burrows was commented upon by Earhart (1969), Van Troostwijk (1976), and Danell (1978b). All observed a significantly greater number of burrows, greater complexity and longer life in soils of finer texture. Fertility indirectly affected distribution (Chulick 1979) and type of burrow (Earhart 1969) by its effect on plant distribution and density. Porosity (Wilson and Killgore 1978) and moisture content (Ognev 1948, Walker 1975, Kay and Whitford 1978) affect the microenvironment of burrowing rodents. Rate of gas exchange from the internal burrow microenvironment is critical to the existence of burrowing rodents. Restrictions on this exchange rate affects the conformation and seasonal occupancy of burrows especially under abnormal environmental conditions. What may have been suitable under dry and warm conditions may become uninhabitable during periods of heavy precipitation and extreme cold. Saturated or frozen soil reduces the rate of gas exchange between the burrow and the external environment.

Adaptations to restrictions imposed by soil characteristics include large chambers and periodic movements to different areas in extensive burrow systems, location of burrows under root structures (Wilson and Killgore 1978), seasonal occupation of burrows (MacArthur and Aleksiuk 1979) and accessory openings throughout the burrow system (Wilson and Killgore 1978).

Territoriality

The existence of territorial behavior was indicated for populations of *O. z. zibethicus* (Errington 1943, Aldous 1947, Sprugel 1951) and *O. z. cinnamominus* (Sather 1958). Studies of territorial behavior in muskrats usually include capture-recapture live trapping data, ear-tagging or banding (Van Troostwijk 1976) and litter inspection (Sather 1958).

The necessity for some form of territorial behavior may be the limitations it imposes on the breeding population of a given area (Errington 1948). This basis for the formation of territories also was suggested by Verner (1977). Verner's "super territory" accurately described the type of territory maintained by dominant burrowing muskrats within a population. Defense, by dominant burrow dwelling muskrats, of an area larger than necessary to support the residents may be a response to instability and seasonality in food availability. The aggressive defense of territorial boundries only during the breeding season by muskrats fits Verner's hypothesis in which this type of behavior is advantagous only when it limits the reproductive efforts of animals in adjoining areas.

Evidence for existence of territoriality is difficult to obtain for many muskrat populations because of their existence at less than saturated population levels (Errington 1948). In many situations mortality due to trapping serves to mask expressions of territoriality (Chulick 1979).

Visible evidence of territoriality took the form of group movements (Dorney and Rusch 1953), intraspecific strife (Errington 1943) and tendency for this strife to nullify reproductive efforts (Errington 1940). The lack of overlaps in summer cruising ranges (Shanks and Arthur 1952) was strong evidence of territorial behavior by muskrats.

Errington (1940) suggested 27.4 m to 45.7 m as the minimum territorial diameter in the best of habitats in Iowa. He also suggested that 7.5 breeding pairs per ha was the maximum density tolerated in well situated populations. Sather (1958) found most territories had a single habitable structure during the summer in Nebraska. An additional dwelling structure and a feeding lodge were added to territories in late summer. During these periods it was suggested that all members of a family lived together peacefully.

Aggressive behavior is the most readily visible evidence of territorial maintenance by muskrats. Shanks and Arthur (1952) mentioned that the dominant, territorial holding residents of small farm ponds will forcibly prevent transients from settling there. Extreme levels of this behavior were observed by Errington et al. (1963) in densely occupied, highly unstable habitat in Iowa.

Population Counts

Censusing of muskrats has taken many forms including strip bed counts, transect counts, roadside surveys, aerial lodge counts, general sign census, spring breeding territory counts, pushup counts and house counts.

In the coastal marshes of Texas, Lay (1945) used total counts of active beds (dwelling lodges) multiplied by 2.5 muskrats per bed to arrive at a permissable harvest quota. He reviewed attempts to census muskrats by transect counts, roadside surveys and aerial lodge counts. Because of difficulties in spotting all inhabited structures, the first 2 methods were considered to be inaccurate. Lodge counting from the air suggested a promising census method (Lay 1945).

Dozier's (1948) house counting procedure involved a simple count of active dwelling lodges. Activity and type of lodge were judged on the presence or absence of external lodge repairs and size. He suggested the number of houses multiplied by the racial litter size provided a population estimate. Dozier et al. (1948) found the number of muskrats per dwelling lodge within an area was remarkably constant from year to year.

Breeding territory counts of muskrats residing in both lodges and burrows were used by Errington (1943) and Sather (1958). Both authors relied on visual counts of centers of activity or "breeding territories". Activity was judged on the basis of freshly repaired lodges, presence of nesting material within the lodge or burrow, old and fresh food cuttings in the vicinity, roiled water in runways and fresh plant materials used in repair of burrows. These counts were then multiplied by a final figure of young per breeding female derived from reproductive success and mortality estimates. These estimates were made from placental scar counts and the ratio of young to breeding female data gathered from trapped carcass examination.

Relative abundance of muskrats was measured by aerial pushup counts (Davydov 1968), aerial and ground counts of house and burrows (Aldous 1947, Smith and Jordan 1977) and the burrow census (Chulick 1979). Each of these systems relied on a change in number of structures from year to year as an indicator of parallel changes in muskrat populations.

Food

Feeding habits of muskrats, as observed by most, indicated that above all else, the muskrat is an opportunistic feeder. Regional diets ranged from complete herbivory to complete carnivory and were related to both availability of food and learned behavior (Errington 1941).

In herbivorous populations there was little or no selectivity at times (Errington 1941) and a marked preference for variety (Butler 1940). This type of feeding behavior was noted throughout the muskrat's range in North America, Europe (Willner et al. 1975) and Sweden (Danell 1977b). A reflection of this behavior was the lack of correlation found between muskrat distribution and number of plant species available (Greenwell 1948, Shanks and Arthur 1952).

Carnivorous populations, wherever they existed, seemed to definitely prefer fresh water clams (Johnson 1925) (common and scientific names are listed in Table 1). Densely populated carnivorous populations in the north central United States had a tendency to develop seasonally cannibalistic feeding behavior (Errington 1939, 1941).

Table 1. Common and scientific names of plants[1] and animals[2] observed and/or mentioned in this study.

Common Name	Scientific Name	Common Name	Scientific Name
American elm	*Ulmus americana*	Cut-leaved water-horehound	*Lycopus americanus*
Annual brome	*Bromus* sp.	Dandelion	*Taraxacum officinale*
Annual dropseed	*Sporobolus neglectus*	Dense flowered water willow	*Justicia americana*
Arrowhead	*Sagittaria Englemanniana*	Duckweed	*Lemna minor*
Barnyard grass	*Echinocholoa crusgalli*	Fall panic grass	*Panicum dichotomiflorum*
Beggar-ticks	*Bidens cernua*	Giant goldenrod	*Solidago gigantea*
Black bindweed	*Polygonum Convolvulus*	Giant ragweed	*Ambrosia trifida*
Bulrush	*Scirpus* sp.	Green ash	*Fraxinus pennsylvanica*
Bur oak	*Quercus macrocarpa*	Ground cherry	*Physalis heterophylla*
Catnip	*Nepeta Cataria*	Hackberry	*Celtis occidentalis*
Cattail	*Typha latifolia*	Hemp	*Cannabis sativa*
Chicory	*Chichorium Intybus*	Horseweed	*Conyza canadensis*
Common sunflower	*Helianthus annuus*	Kentucky bulegrass	*Poa pratensis*
Cottonwood	*Populus deltoides*	Lamb's quarters	*Chenopodium album*
Creeping bent	*Agrostis palustris*		

Table 1 --Continued.

Common Name	Scientific Name	Common Name	Scientific Name
Long-leaved pondweed	Potamegeton nodosus	Smooth brome	Bromus inermis
Many-flowered aster	Aster ericoides	Summer-cypress	Kochia scoparia
Musk thistle	Carduss nutans	Tall dropseed	Sporobolus asper
Partridge-pea	Cassia fasciculata	Tall thistle	Cirsium altissimum
Prairie rose	Rosa suffulta	Water hemlock	Cicuta bulbifera
Prairie sunflower	Helianthus petiolaris	Water smartweed	Polygonum natans
Prickly lettuce	Lactuca serriola	White avens	Geum canadense
Red-rooted cyperus	Cyperus erythrorhizos	Wild plum	Prunus americana
Reed canary grass	Phalaris arundinacea	Willow	Salix sp.
Scribner's panicum	Panicum scribnerianum	Yellow foxtail	Setaria glauca
Sedge	Carex sp.		
Stiff goldenrod	Solidago rigida		
Stinging nettle	Urtica dioica		
Smartweed	Polygonium lapathifolium		

Table 1 --Continued.

Common Name	Scientific Name
Canada Goose	*Branta canadensis*
Crayfish	*Orconectes* sp. and *Cambarus* sp.
Fresh water clam	*Anodonta* sp.
Hawks	FALCONIFORMES
Mink	*Mustela vison*
Otter	*Lutra canadensis*
Owls	STRIGIFORMES
Raccoon	*Procyon lotor*
Weasels	*Mustela* sp.

1 From Gleason and Cronquist (1963)

2 From Kiviat (1978)

Number of plant species, both terrestrial and aquatic, that were utilized within a normal population, were many. Field observations in New York provided a list of 26 species harvested by muskrats (Johnson 1925). Feeding platform sampling in Maine indicated that 36 species were utilized by a marsh dwelling population (Takos 1947). Food studies in China listed 107 species of food taken, 93.4% of which were plants (Ching and Chi-Tang 1965).

Preference for specific plant parts was related to seasonal availability and palatability (Johnson 1925, Errington 1939, Butler 1940). Plant availability was also correlated with body size. Small body size within a population was indicative of limited plant availability whereas large body size indicated satisfactory but seasonal plant availability (Boyce 1978). When seasonal availability was combined with limited abundance, the number of litters decreased, the number of young per litter decreased and the physical condition of adults deteriorated.

Inaccessibility caused by environmental constraints may cause muskrats to selectively harvest peripheral plant stands (MacArthur 1978).

Plant availability, both seasonal and absolute, was strongly correlated with water availability (Beard 1973) and water depth. A depth of 1.2 m or more, prevented growth of most heavily utilized emergent aquatic plants (Errington 1948).

Muskrat carrying capacity compared with aquatic plant density was described by Butler (1940). Cattail densities of 41.98 stems/m^2 supported 57.5 muskrats/ha, bulrush densities of 3.95 stems/m^2 supported 42.5 muskrats/ha, while sedge densities of 90.06 stems/m^2

supported only 7.5 muskrats/ha.

Sign

Indications of muskrat activity are readily discernible throughout the occupied sectors of its native and adopted range. Structures of the muskrat including dwelling lodges, feeding lodges, pushups, feeding platforms and burrows are usually the first sign noticed. Other sign provides an indication of activity levels and movements.

Food scraps 10 to 25 cm long may be found in the vicinity of habitations and favored feeding areas (Johnson 1925, Van Troostwijk 1976, Danell 1977a). Scat piles were often found on any exposed, elevated and accessible surface (Johnson 1925, Dozier 1948). Channels leading to burrows or lodges would, when actively used, contain roiled or muddy water (Dozier 1948). Ice over actively used channels in winter contained concentrations of bubbles (Warwick 1936). Tracks on suitable banks were readily detectable and were a reliable indication of both presence and level of activity of muskrats. During the spring breeding season it was possible to detect the odor of muskrats in inhabited structures (Van Troostwijk 1976).

Predation

Recognized predators of muskrats include raccoons, weasels, otters, hawks, and owls (Johnson 1925, Lay 1945). In many cases predation was confined to stressed or concentrated segments of the population (Gerell 1970) or to simple scavenging of diseased or dead muskrats (Sather 1958).

Mink predation upon muskrats was generally not severe but varied from area to area (Johnson 1925). Level of predation was subject to environmental influences such as drought or severe cold (Errington 1939, Bellrose and Low 1943). On some occasions, especially with well situated muskrat populations, mink-muskrat confrontations were won by either party (Errington 1939). Even a mutalistic relationship could develop between neighboring muskrats and mink as suggested by the simultaneous occupation of muskrat burrows by members of both species (Errington 1937a, Kiviat 1978).

Raccoon predation on muskrats might be related to their opportunistic feeding (Fritzell 1978). They dig into lodges especially during the muskrat breeding season (Lay 1945) but seem incapable of preying on burrow dwelling muskrats (Wilson 1953). Wilson indicated that the level of predation was often area specific. These factors plus Fritzell's (1978) statement that young raccoons were extremely inefficient foragers suggest that given a mobile, well-situated prey species, such as most populations of muskrats, raccoon predation would be of minor importance. Predation that did occur could probably be attributed to fortuitous circumstances or learned behavior by raccoons.

Reproduction

The initiation of breeding of muskrats was prompted by the spring thaw (Errington 1963), changes in air temperature (Sprugel 1951) and increased precipitation (Olsen 1959). These efforts were followed by the first peak in litter production commencing in March in the Netherlands (Van Troostwijk 1976), the first half of April in northwestern Iowa (Errington 1937b) and Wisconsin (Beer 1950), late April to early May in north central Nebraska (Sather 1958) and late May in

Quebec (Stewart and Bider 1974). The initial peak was followed, at 1 month intervals, by 1 to 2 additional peaks (Errington 1937b).

The reported mean litter size of both O. z. zibethicus and O. z. cinnamominus was relatively constant throughout their ranges. Reviewed litter sizes ranged from 6.0 young/litter for adult breeding females in Nebraska (Sather 1958) to 7/litter for muskrats in northern Russia (Geller and Skrobov 1967).

The number of litters per adult breeding female/year seems roughly correlated with the length of the ice free season. Some of the reported estimates were 2 in Quebec (Stewart and Bider 1974), 2 to 3 in northern Russia (Geller and Skrobov 1967), 2.5 to 2.7 in Nebraska (Sather 1958) and 3.25 in the Netherlands (Van Troostwijk 1976).

The maximum annual net reproductive rates reviewed was 19 young/breeding adult female, reported for an ideally situated population in Iowa by November (Errington 1937b). This may be contrasted with the annual net reproductive rate of 5 young/adult breeding female by November, living under less than ideal conditions in Quebec (Stewart and Bider 1974).

RESEARCH AREA

Field work was conducted at Branched Oak Recreation Area located in northwestern Lancaster county Nebraska at 96° 52' N. latitude, 40° 52' W. longitude (Figure 1). The recreation area encompassed 2,238 ha which included a 720 ha lake and 1,518 ha of land used for wildlife management and recreation. The area is intensively used for such outdoor activities as boating, water skiing, fishing, camping and hunting. The user rate approaches an estimated 1,000,000

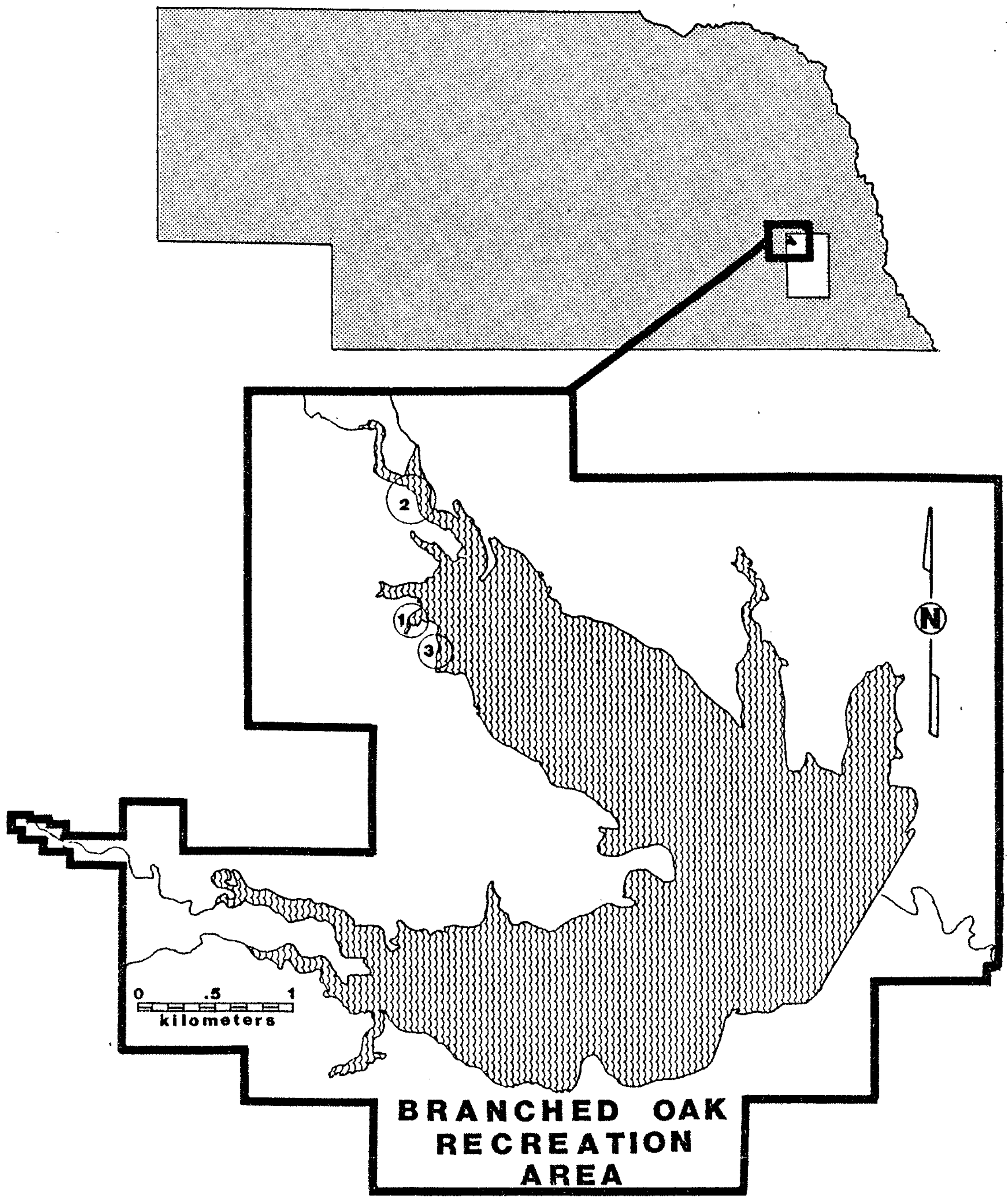

Figure 1. The location of Branched Oak Recreation Area in Lancaster county, Nebraska. Study Areas indicated by circled numerals.

visitations per year.

The recreation area lies within the long rolling hills of eastern Nebraska. It is characterized by narrow rounded ridges with short side slopes intersected by numerous well defined drainage ways.

Soils are primarily eolial and alluvial and originated from Pleistoncene glacial deposits. Cretaceous sandstone deposits form the bedrock (Table 2).

Climate is characterized by cold winters and warm to hot summers, with highly seasonable moderate precipitation. Three-fourths of the annual precipitation falls during the April through September growing season. Prevailing winds are from the north in the winter months and generally from the south during the rest of the year (Table 3).

Study Areas

The selection of 3 study areas began with the location of sections of shoreline separable on the basis of gross soil texture of the surface horizons (loam, clay and sand) and slope of the substrate. Areas composed of soils not readily classified by inspection and/or areas with long (20 m) slopes of less than 5 degrees were rejected.

The limited number of choices allowed by the above requirements prompted the selection of 3 closely associated areas on the north fork of the lake. Boundaries of areas were initially delineated by some physiographic or edaphic impediment to burrowing activity.

Study Area 1

Study Area 1 is an inlet on the west shore of the north fork of the lake (Fig. 2). It forms the boundary of the alluvial plain to the

Table 2. Soil types and phases in the study areas.

Soil series and phases[1]	Depth of typical profile (cm)	Percentage of particles less than[2] (mm)				USDA texture[2]	Slope (%)	Physiographic position	Parent material
		4.7	2.0	0.05	0.002				
Breaks-Alluvial land complex	--	--	--	--	--[a]	SS	11-30	Upland drainage ways	Glacial till
	--	--	--	--	--	SCL			
	--	--	--	--	--	SCL			
BpF[a]	--	--	--	--	--	SS	11-30	Upland drainage ways	Glacial till
	--	--	--	--	--	SCL			
	--	--	--	--	--	SCL			
Crete	33.0	--	--	94	18-27	SL	0-4	Uplands and terraces	Peorian loess
	81.3	--	--	97	40-45	SC			
	152.4	--	--	97	27-35	SL			
CrB	27.4	--	--	94	23	SCL	1-2	Uplands	Peorian loess
	62.7	--	--	97	43	SC			
	152.4	--	--	97	31	SL			
Dickinson	91.5	--	100	51	12	FDSL	5-20	Uplands and footslopes	Sandy glacial loess
	152.4	--	100	4	4	SD			
DcD	152.4	--	100	4	4	SD	6-20	Uplands and footslopes	Sandy glacial loess
Judson	71.1	--	--	88	21	SL	2-6	Upland footslopes	Mixture of loess, alluvium and colluvium
	152.4	--	--	95	34	SCL			

Table 2 --Continued.

Soil series and phases	Depth of typical profile (cm)	Percentage of particles less than (mm) 4.7	2.0	0.05	0.002	USDA texture	Slope (%)	Physiographic position	Parent material
JuC	71.1	--	--	88	21	SL	2-6	Upland footslopes	Mixture of loess, alluvium and colluvium
	152.4	--	--	95	34	SCL			
Kennebec	17.8	--	--	93	17	SL	0-1	Bottomland	Silty alluvium
	152.4	--	--	94	16	SL			
Ke	17.8			93	17	SL	0-1	Bottomland	Silty alluvium
	152.4			94	16	SL			
Morrill	35.6	--	100	57	20	CL	3-15	Upland valley sides	Weathered and leached glacial till
	73.7	--	100	52	24	CL			
	152.4	--	100	31-37	17-21	SL			
MrD	35.6	--	100	57	20	CL	6-11	Uplands	Weathered and leached glacial till
	73.7	--	100	52	24	CL			
	152.4	--	100	31-37	17-21	SL			
MrD2[b]	16.5	--	100	57	20	CL	6-11	Uplands	Weathered and leached glacial till
	85.1	--	100	52	24	CL			
	152.4	--	100	31-37	17-21	SL			
Steinauer	15.2	95-100	85-95	49	27-35	CL	8-30	Uplands	Kansan till
	152.4	100	85-95	69	27-35	CL			
StF	15.2	95-100	85-95	49	27-35	CL	17-30	Uplands	Kansan till
	152.4	100	85-95	69	27-35	CL			

Table 2 --Continued.

Soil series and phases	Depth of typical profile (cm)	Percentage of particles less than (mm) 4.7	2.0	0.05	0,002	USDA texture	Slope (%)	Physiographic position	Parent material
Zook	50.8	--	100	92-95	30-33	SCL	0-1	Bottomland	Silty and clayey alluvium
	165.1	--	100	93	37	SC			
Zp	50.8	--	100	92-95	30-33	SCL	0-1	Bottomland	Silty and clayey alluvium
	165.1	--	100	93	37	SC			

1 Soil phases represented by accepted abbreviations.

a Slope designation. B=1 to 5%, C=2 to 7%, D=6 to 20%, F=11 to 30%.

b Erosion designation. 2=eroded, 3=severely eroded.

2 Gravel>2mm, 2mm=Sand>0.05, 0.05=Silt>0.002mm, Clay<0.002mm.

3 CL=Clay loam, FDSL=Fine sandy loam, SC=Silty clay, SCL=Silty clay loam, SD=Sand, SL=Silt loam, SS=Silty sediment.

a Too variable to be classified.

From Beesley et al (1948), Elder (1969) and Quandt (1974).

Table 3. Temperature, percipitation and wind speed during 1977.

	TEMPERATURE (^{o}C)						PRECIPITATION (cm)				
	Mean				Extremes						
	Daily			Normal[1]					Normal	Record Mean	
Month	Max	Min	Monthly	Monthly	Max	Min	Total	Snow	Total	Total	Snow
J	-3.9	-17.1	-10.5	-5.4	5.5	-28.3	1.60	22.10	1.85	1.80	17.27
F	8.6	-8.9	-0.2	-2.3	20.5	-18.9	0.20	0.25	2.90	2.50	15.75
M	13.1	-0.3	6.4	2.5	26.1	-13.8	8.99	21.08	3.91	3.71	14.99
A	20.6	6.8	13.7	10.7	28.9	-2.8	4.65	8.64	6.58	6.30	2.29
M	26.6	13.8	20.2	16.7	32.2	6.7	13.21	---	9.83	9.75	0.25
J	30.4	16.7	23.6	22.2	36.7	9.4	2.51	---	13.11	10.87	---
J	34.0	20.3	27.2	25.2	38.9	10.6	9.53	---	8.23	9.14	---
A	28.1	16.7	22.4	24.2	33.9	11.7	19.00	---	9.22	8.64	---
S	25.1	13.1	19.1	18.7	31.7	7.2	15.37	---	8.25	7.70	---
O	17.2	4.4	10.8	12.7	24.4	-3.9	4.72	---	4.29	4.75	0.76
N	9.4	-2.4	3.5	3.9	17.8	-13.9	5.16	8.38	2.48	3.07	6.86
D	2.1	-9.8	-3.8	-2.6	15.0	-21.1	0.89	9.40	2.01	2.08	14.00
Year	17.6	4.4	11.1	10.5	38.9	-28.3	85.83	60.60	72.67	70.31	72.14

Table 3--Continued.

	WIND SPEED (km/hr)				
	Mean			Maximum	
Month	Direction	Speed	Normal[2] Speed	Direction	Speed
J	NW	17.4	15.9	N	72.4
F	NW	16.1	17.2	NW	75.6
M	SW	21.1	19.3	SE	69.2
A	SW	19.3	20.9	SW	67.6
M	SSE	17.7	17.1	SE	67.6
J	SE	16.6	16.4	N	56.3
J	S	20.0	16.9	N	77.3
A	SSE	15.5	16.4	N	95.0
S	SE	15.1	15.5	SE	54.7
O	N	15.6	15.9	N	54.7
N	WNW	17.4	16.6	NW	72.4
D	NW	17.7	15.8	NW	61.2
Year	SW	17.4	17.1	N	95.0

1 Based on the record for the 1941-1970 period.

2 Based on the record for the 1972-1977 period.

From U.S. Weather Bureau. Station 14939 Lincoln, Nebraska, 40° 51' N. latitude, 96° 45' W. longitude, 359 m above m.s.l.

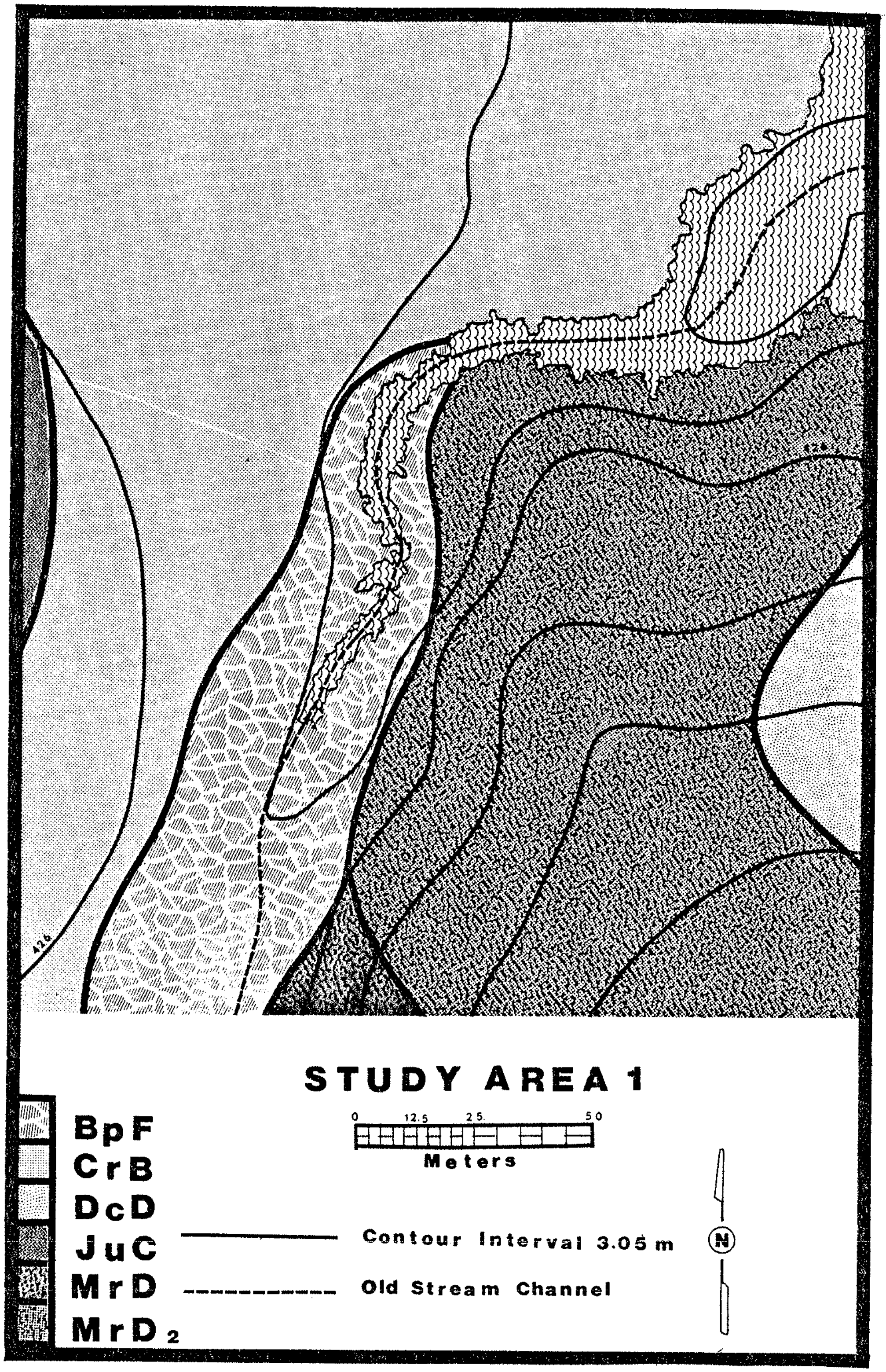

Figure 2. Soil phases and topography of Study Area 1.

northeast and the breaks to the southwest. It is bounded by the canyon-like walls of an inundated intermittent stream bed.

The inlet varies from approximately 40 m wide and 5 m deep at the open end to 3 m wide and 0.8 m deep at the upper end. Both the south and north above-water banks are abrupt and eroded. The inlet bottom is U-shaped and relatively smooth.

Soils along the southern and eastern shore range from Dickinson fine sand at the open end to a mixture of Morrill clay loam and Breaks-Alluvial silt at the upper end. The limited flood plain consists of alluvial silt mixed with sand at the lower end and silty alluvium at the upper end.

Soils along the northern and western shore are primarily Crete silty-clay loam, with a limited amount of Breaks-Alluvial silt at the extreme upper end. The limited floodplain that occurs on the south bank is located near the outlet to the lake.

Study Area 2

Study Area 2 is on the south bank of the north fork of the lake (Fig. 3). Its downstream end marks the zone of transition between the stream and the main body of the lake. The upstream end is approximately 250 m downstream from the junction of the north and south fork of the north branch of Oak Creek. The stream bed bisects a broad and nearly level lowland terrace.

The inundated stream bed is bounded by the gradually to moderately sloping original floodplain. Present banks are moderately to abruptly sloping and highly convoluted. These irregularities result in many small inlets and bays that greatly increase the bank length to water ratio.

The predominant soil phases on the northern shore are Silty Alluvium and Kennebec silt loam. Both soils are alluvial in origin and therefore relatively uniform.

Zook silty clay loam is the soil phase on the southern shore. This soil phase is located on the lowland terrace and includes a limited number of small clay outcrops.

Study Area 3

Study Area 3 is located on the western shore of the lacustrine section of the north fork of the lake (Fig. 4). It is bounded on the west by a steep, severely eroded, tree covered ridge. It is bounded on the east by the submerged flood plain of the north branch of Oak Creek.

The sandy footslope nature of the shoreline at the base of the bluff combined with substrate movement caused by wave action results in a gradually sloping inundated substrate through most of the area. This slope increases at the northern end of the study area as the inundated stream channel approaches the shore.

The substrate in Area 3 is the result of erosion of the ridge. The soil phase of the ridge is a severely eroded Dickinson fine sand with occasional outcrops of cobble to boulder size stones. The northern boundary of the study area is marked by a ridge of stones that have collected along the shoreline.

WETLAND CLASSIFICATION

Study Area 1

Study Area 1 is a lower perennial, riverine system with a continuous

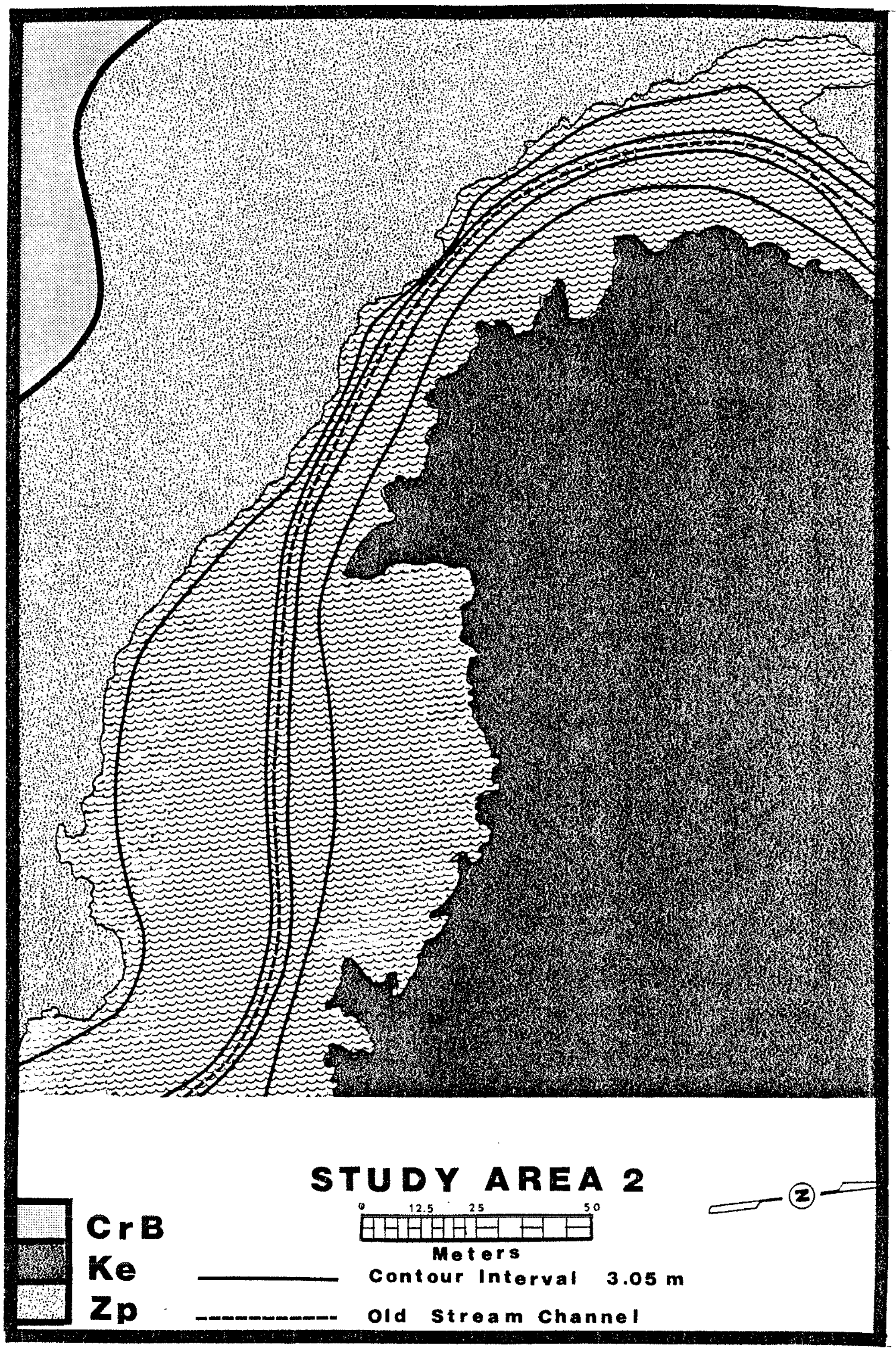

Figure 3. Soil phases and topography of Study Area 2.

Figure 4. Soil phases and topography of Study Area 3.

but irregular flow (Cowardin et al. 1977). The lower perennial subsystem is atypical in that almost all of the flowing water results from the discharge of many springs on the west bank and that the gradient of the bottom approaches that of an upper perennial subsystem.

The inundated stream channel falls into the classification, permanently flooded stream bed, subclass mud. The silt bottom is smooth and rooted hydrophytes are very sparsely distributed. This central area is bounded on its southwestern end by emergent wetland dominated by a nonpersistent intermittently exposed to seasonally flooded stand of arrowhead. The northern and southern shorelines are classified as intermittently exposed to seasonally flooded dead forested wetland dominated by American elm and green ash. Forested areas are bordered by and contain submergent vascular beds of pondweed and free-floating beds of duckweed. Shoreward edges of both the forested wetland and aquatic beds are occupied by nonpersistent emergent wetlands dominated by arrowheads (Fig. 5).

Study Area 2

Study Area 2 is a lower perennial riverine system with a regular to seasonally irregular flow. The inundation of the lower floodplain, brought about by damming of the channel has resulted in many backwater areas of limited or no flowage.

The permanently flooded mud stream channel has a relative smooth bottom that is occasionally interrupted by stumps and other debris resulting from land clearing operations that took place during construction of the lake. The channel is bounded on both the north and south

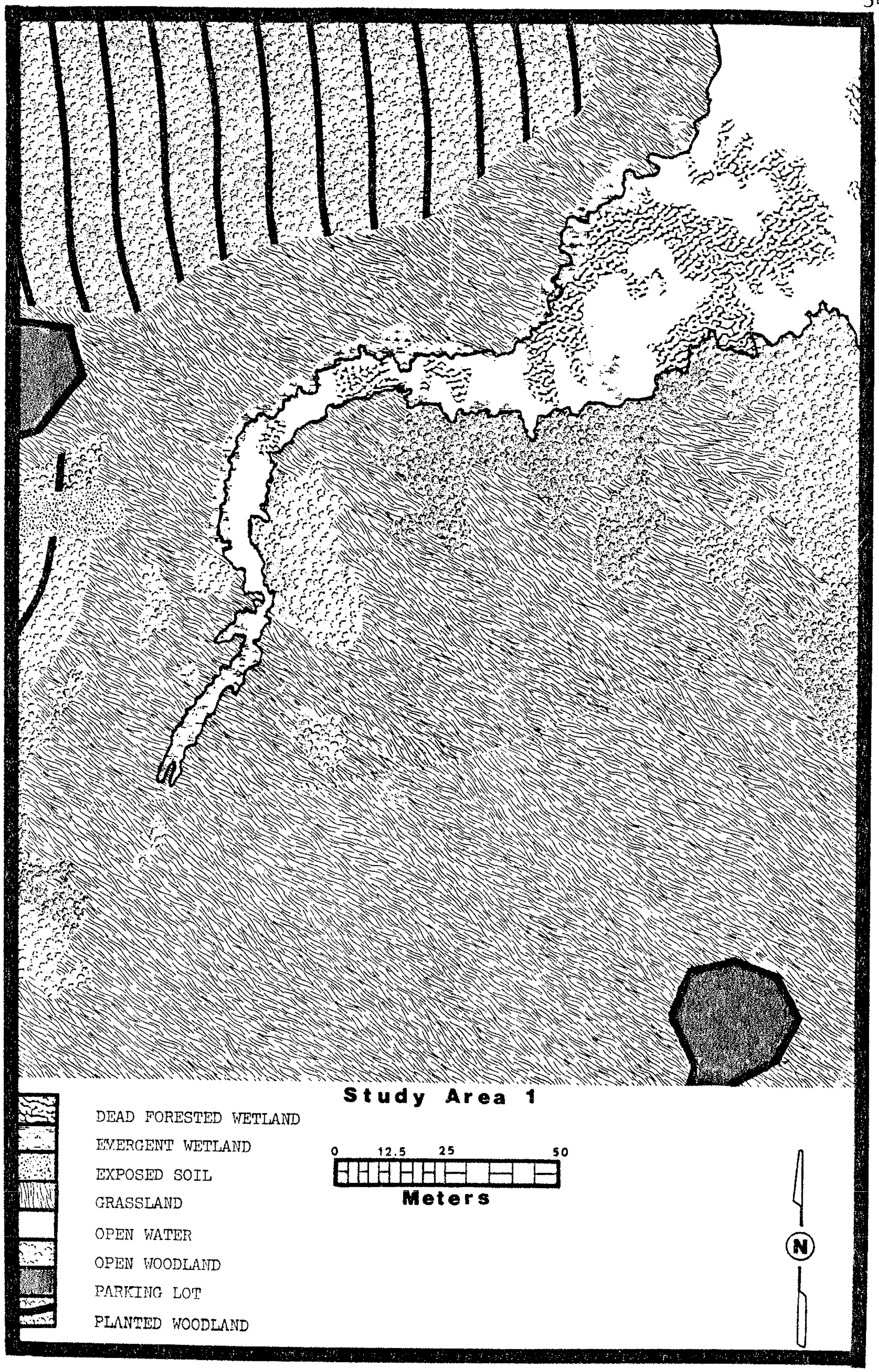

Figure 5. Wetland and terrestrial plant communities of Study Area 1.

sides by intermittently exposed to seasonally flooded dead forested wetlands dominated by cottonwood, American elm, hackberry and green ash. These forested wetlands also contain aquatic beds of floating-leaved pondweed and floating mats of duckweed. The forested wetlands and aquatic beds are bounded on the landward sides by persistent emergent wetlands dominated by cattails and nonpersistent emergent wetlands dominated by arrowheads. On the southern shore these emergent wetlands are superseded by semi-permanently flooded to seasonally flooded vegetated flats dominated by smartweed (Fig. 6).

Study Area 3

Study Area 3 is a littoral, lacustrine system sharply delineated by the limnetic zone of the inundated stream bed to the east and by sharply rising bluffs to the west. The meandering stream channel results in extreme variability in the extent of the littoral zone.

The major portion of the area can be classified as permanently flooded to intermittently exposed unconsolidated sand bottom. The permanently flooded to seasonally flooded aquatic bed is represented, to a limited extent, by floating-leaved pondweed and floating mats of duckweed. Intermittently exposed to seasonally flooded non-persistent emergent wetlands dominated by arrowhead are present in the protected convolutions of the shoreline. Patches of permanently flooded to seasonally flooded dead forested wetland dominated by bur oak defines the floodplain of the stream channel (Fig. 7).

MATERIALS AND METHODS

Benchmarks within the study areas were the center of the first

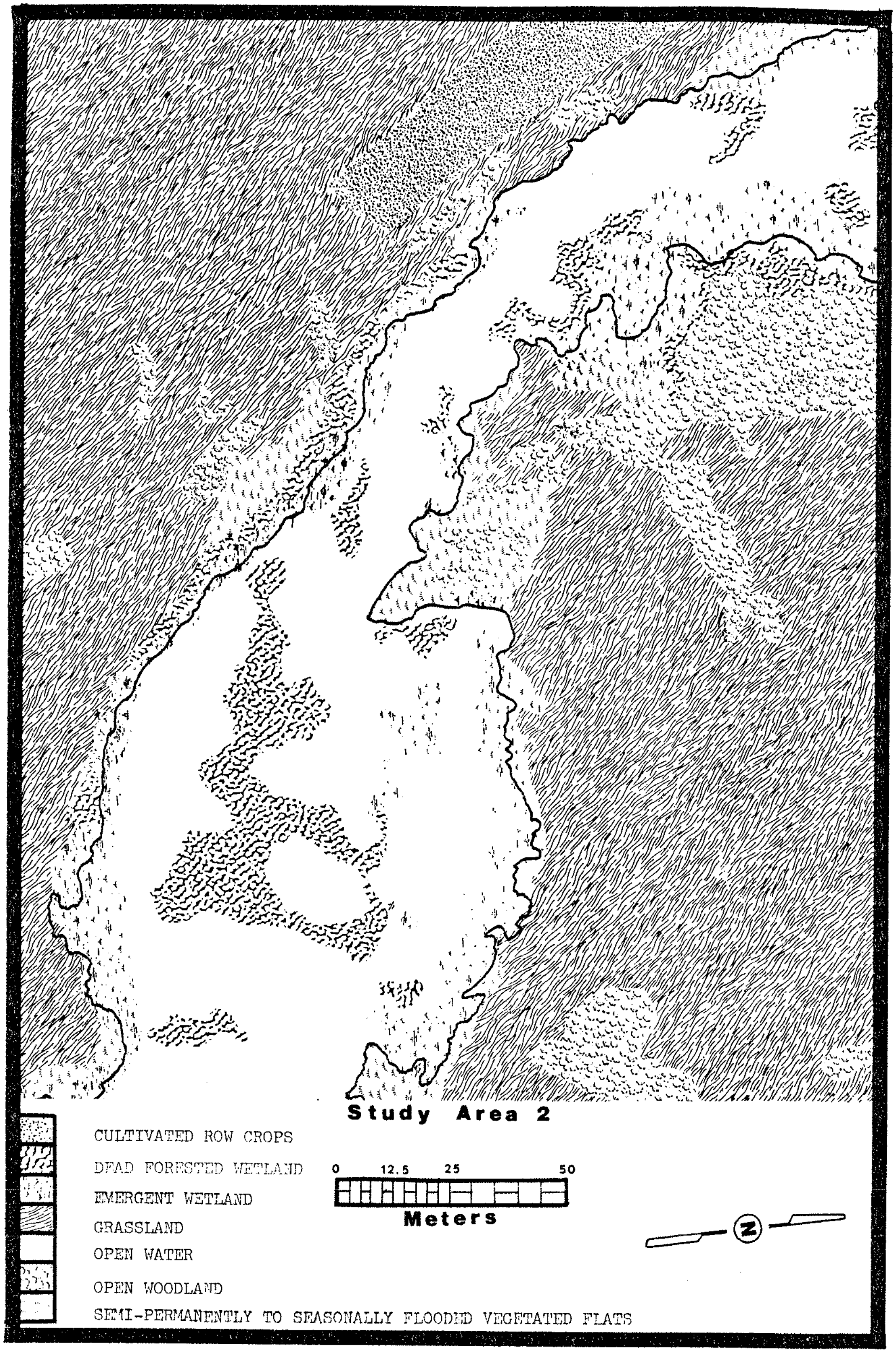

Figure 6. Wetland and terrestrial plant communities of Study Area 2.

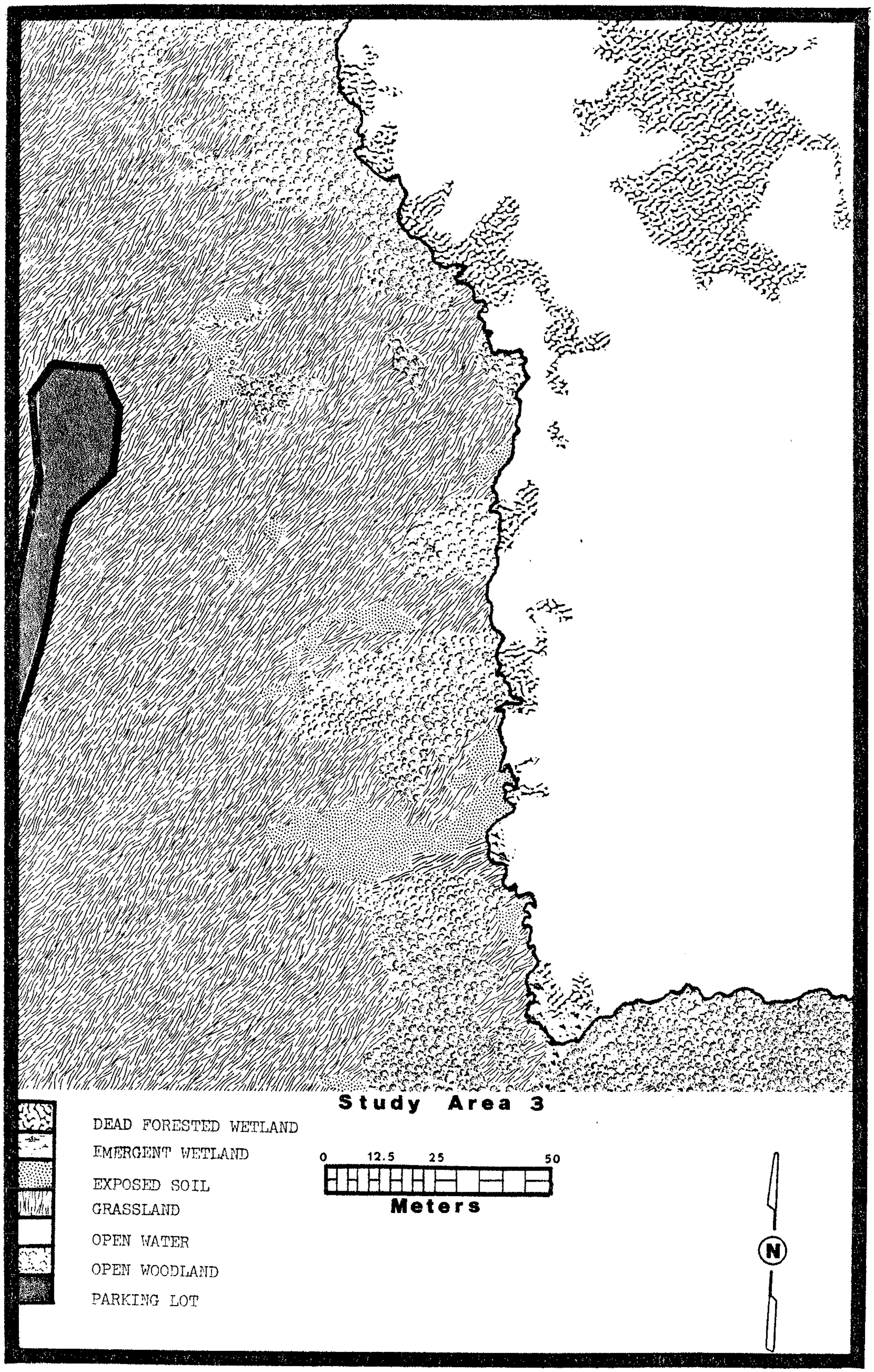

Figure 7. Wetland and terrestrial plant communities of Study Area 3.

burrow opening nearest to the east boundary of Study Area 1 (Fig. 8), the east boundary of Study Area 2 (Fig. 9) and the north boundary of Study Area 3 (Fig. 10).

Four methods were used to locate burrows. The first was a simple visual inspection for burrow openings. This inspection was made while wading on a parallel line, 1 to 2 m from the shore. The second method involved a generalized search for underwater openings by feeling for them with the feet. This search was carried out on the submerged substrate bounded by the shoreline on 1 side and by 1.5 m deep water on the other. The third method consisted of feeling for openings with hands in water up to 0.8 m deep. The last method consisted of probing the substrate with a pointed 1.27 cm X 1 m iron rod (Warwick 1936). Probing was carried out on the substrate between the shoreline and 1 m deep water.

Each burrow opening, when initially located, was marked with a red plastic road flag (10.2 X 11.4 cm) attached to a 0.9 m wire. After each inspection trip each burrow was assigned to 1 of 3 burrow types approximately equal to Earhart's (1969) feeding, winter and breeding categories. Determinations were made visually or by feel on the basis of presence and length of tunnels. Burrows were then marked with a second plastic flag, either red or yellow, to signify the winter or breeding category or left with the initial yellow flag to signify the feeding category.

Measurements taken in the burrow location and excavation portion of the study were made with a 2 m hand held metal tape, 5 m metal logger's tape and a 50 m fiberglass reel tape. Plotting measurements were made with the 50 m fiberglass tape, an optical range finder with

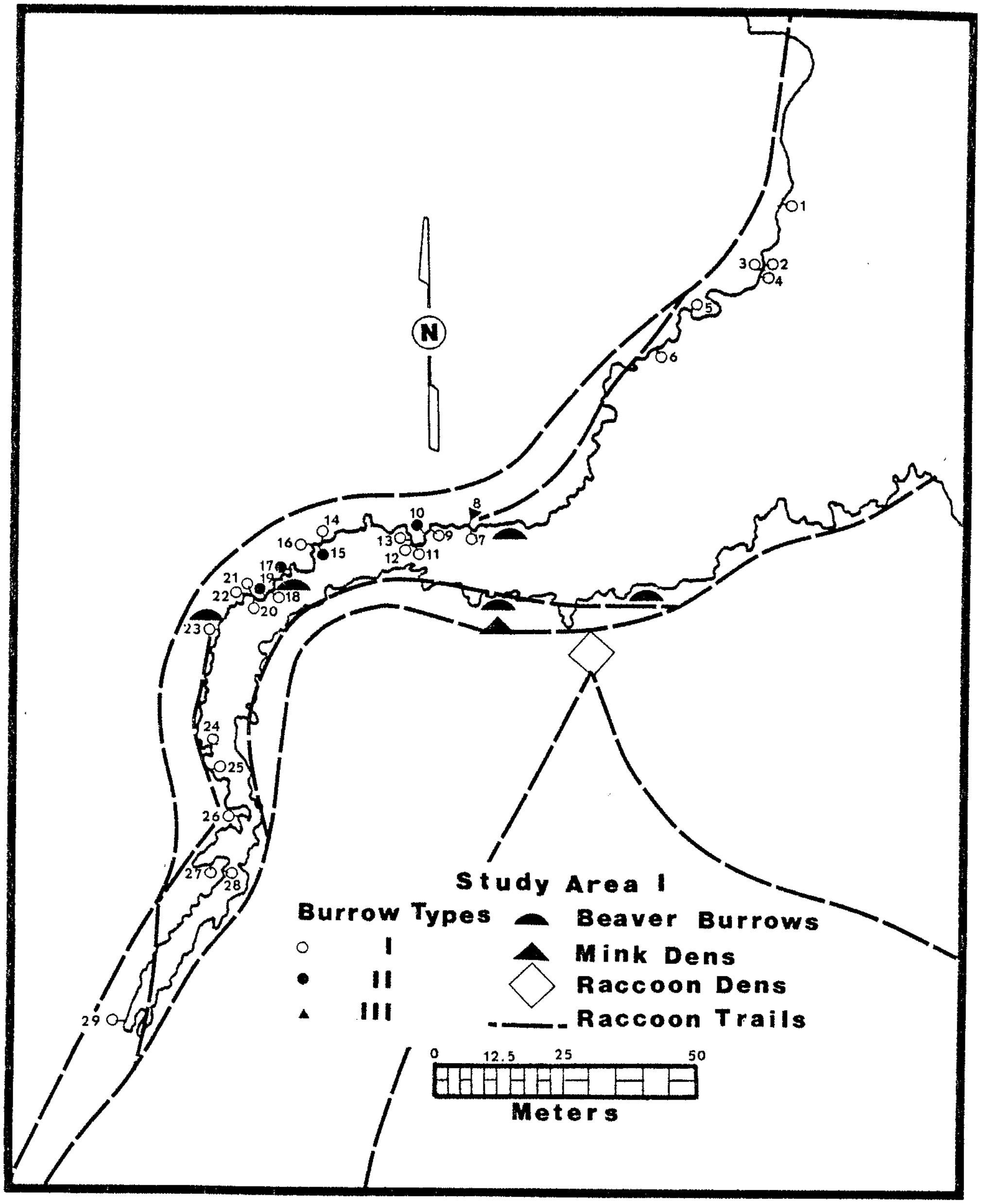

Figure 8. Distribution of muskrat burrow types and animal activity patterns in Study Area 1.

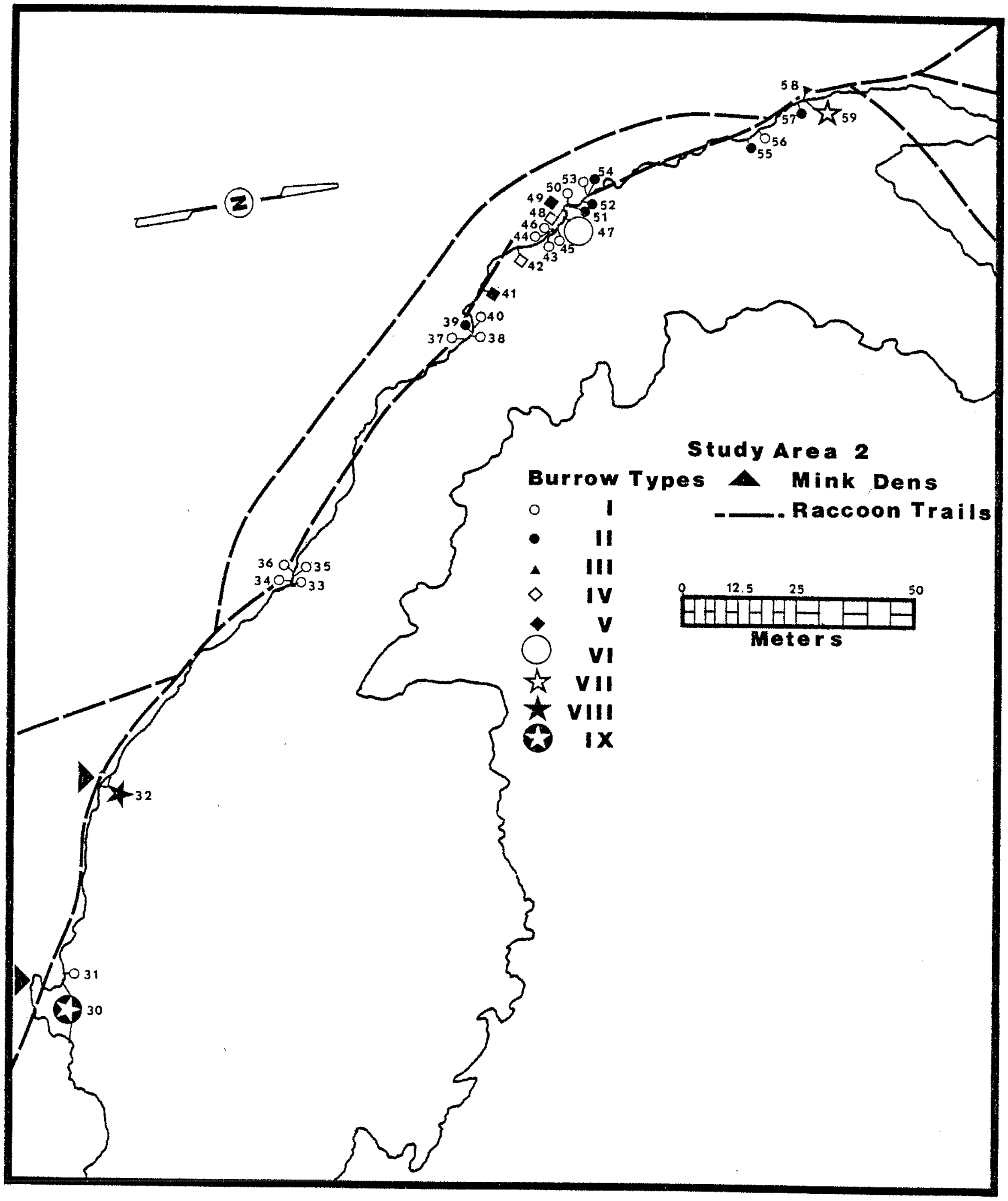

Figure 9. Distribution of muskrat burrow types and animal activity patterns in Study Area 2.

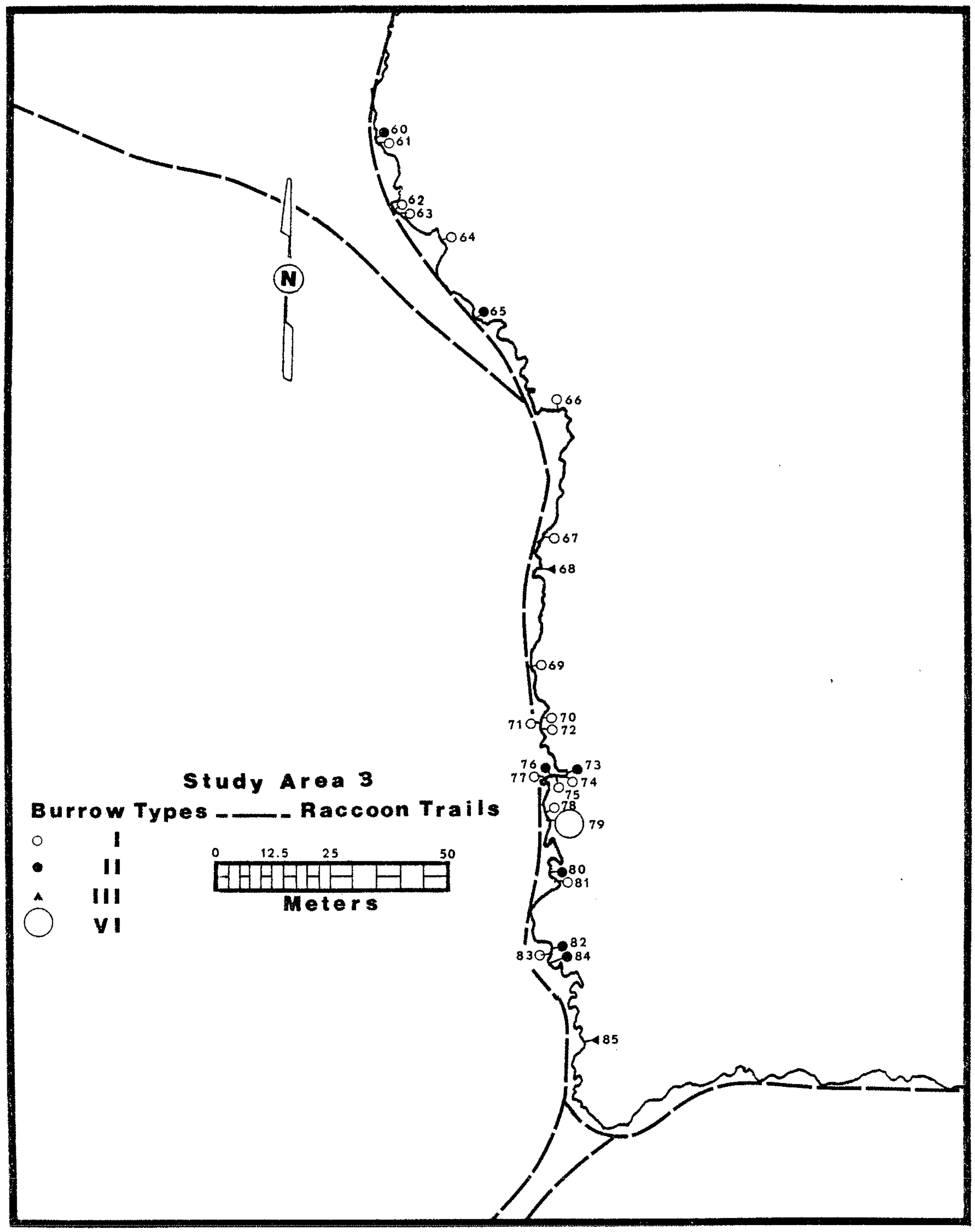

Figure 10. Distribution of muskrat burrow types and animal activity patterns in Study Area 3.

a 17.4 to 183 m ranging capacity and a Suunto hand-held compass. Some of the bank slope measurements were made with a Suunto hand-held clinometer.

Tools used in excavation of burrows included a drain spade, garden spade, and small garden trowel. Tools used in clearing of vegetation included a machete with a brush hook, axe-mattock, large axe-adz, bow saw and garden hoe.

Tools and other materials were carried in a large trapper's pack basket. Addition of a tempered-hardboard lid provided a stable writing surface.

Burrow Excavation

Data gathered in this portion of the study were used to categorize burrows on the basis of external and internal quantitative parameters. These parameters fell into 3 basic groups: externally discernible burrow characteristics, internal burrow structures and external physiographic, edaphic and biotic variables.

External burrow characteristics measured or recorded included type (Earhart's), number, width and height of openings, distance between openings within a burrow system, distance to nearest opening in an adjacent burrow system, height of opening above water level and position of opening within the study area.

Opening width measurements were taken at the point of maximum extent on a line paralleling the water surface. Opening height measurements were taken on a line perpendicular to, but not necessarily intersecting, the width measurement line. Height of opening above water level was the vertical distance between the base of the above mentioned perpendicular line and the water's surface. All positional measurements were taken from the center of the opening.

Internal burrow structures, counted and measured, included chambers and tunnels. Chamber length, width, height above water level and distance it penetrated the bank were measured. Soil overburden above chambers was also noted. Tunnel widths, length and types were recorded.

Chamber length measurements were taken on the longest axis at the vertical midpoint. Determination of chamber height above water was made by digging a narrow trench to a depth just below water level, from the shoreline to a point just below the edge of the chamber. The distance from the water surface in the trench to the bottom of the chamber was measured. Penetration was measured from the shoreline to the point of maximum penetration of the chamber on a horizontal line intersecting the shoreline at right angles. The overburden was measured from the highest point of the chamber to the soil surface.

Tunnel length measurements were made along the center of the floor of the tunnel from the opening or junction at the beginning, to the chamber or junction at the end. Tunnel widths were measured on a horizontal line bisecting the vertical center point of the tunnel at 2 to 5 locations. The mean of these measurements was then used to represent the overall tunnel width.

The 3 types of tunnels recognized were straight, cross and diagonal. The straight tunnel penetrated the bank at right angles to the shoreline. The cross tunnels paralleled the shore line. The diagonal tunnels ran at a 30 to 60 degree angle to the shoreline.

External physiographic and edaphic features recorded included bank slope, soil texture and other physical features affecting burrow distribution.

Initial bank slope measurements were made with a hand held clinometer. This method was abandoned because of difficulties in maintaining a constant aiming point. The second method consisted of deriving the bank slope from the trigonometric relationship of penetration, chamber height above water level, mean chamber height and soil overburden.

In all cases sand and clay were easily discernible by visual inspection. Loam textural class, although less homogenous than sand or clay, was visually classifiable.

Physical anomalies affecting suitability of the substrate as burrowing material were recorded and in some cases measured. These features included boulder and cobble outcroppings, small areas with frequently occurring land slides, somewhat larger areas subject to extreme erosion, logs, tree roots and occurrences of springs or seeps.

Biotic influences recorded included occurrences of dense root mats or root clumps, and animal activity patterns. Human activity within study areas was also noted.

Signs of Activity

Muskrat activity within the Research Area was regularly monitored. Activity within and in the vicinity of the study areas was checked 1 to 6 times a week from 1 September 1975 to 13 November 1976. Feeding scraps, tracks, burrowing activity, fresh scat deposits and green plants or fragments above water level within a burrow were all considered to be signs of recent activity.

Feeding activity of muskrats is the most evident sign of their presence within an area. Green food scraps 10 to 25 cm long were easily detected at the harvesting site and near or in burrows or other refuges used for feeding.

Tracks near the water line and on trails leading to food sources were used as indicators of recent activity. Tracks were regularly seen in Study Area 2. Recognizable tracks occurred infrequently in Study Areas 1 and 3.

After all burrows in each of the 3 study areas were marked, any new burrows were readily observable. Extremely cloudy water along the bank in still water sections of Study Areas 1 and 2 were an additional sign of recent digging efforts. Presence of fresh cut root material in Study Area 3 on or floating near the shoreline was a useful but infrequently observed indicator of burrowing activity.

In Study Areas 1 and 2 muskrats deposited droppings on floating logs and small peninsular mud flats. Droppings were removed and new deposits were checked for periodically. Muskrats residing within these 2 areas were attracted to specific logs and mudflats and deposited droppings on them almost exclusively.

In the first few active burrows dug in Study Area 2 it was found that living duckweed was present on walls of tunnels above water line. It is probable that these deposits resulted from muskrats swimming through the dense mats of duckweed that characterized the area and then, upon entering the tunnel, any plants adhering to its pelt were deposited on the walls. Whatever the mechanism of its deposition, duckweed was not found on walls of clearly inactive burrows at any point above water line.

Live Trapping

A live trapping, tagging and recapture campaign was initiated in the Research Area. The aim of this effort was to establish the number of occupants per burrow, the constancy of occupancy and the category of usage of each burrow type.

The live trapping effort began with the construction of a prototype family live trap patterned after Snead's (1950). After testing the prototype live trap it was found, that for extended use, reinforcement and some minor modifications in dimensions were necessary. These changes included a heavier gauge sheet metal bottom, aluminum and galvanized metal angle reinforcement on all edges of the middle and upper sections, diagonal aluminum angle bracing between the middle and upper sections, and a sheet metal enclosure for the drop door in the holding cage. These changes were incorporated in the construction of 3 additional live traps.

A rectangular handling cage enclosed on 2 sides and 1 end with 1.27 cm hardware cloth and on the bottom by a 1.9 cm thick board, was made following Snead's pattern (1950). A moveable lid of flat aluminum strip and 1.27 cm mesh hardware cloth was fitted to the open top of the rectangle. This lid was slightly convex from side to side. Wooden dowels 9.5 mm in diameter by 22.9 cm long were pointed on one end and had 1.9 cm diameter by 7.3 cm long dowels attached at the other end. These t-shaped assemblies were used to secure the curved moveable lid at whatever position necessary to immobolize the animal being handled.

The prototype and 3 modified live traps were used for 45 trap nights in Study Areas 1 and 2 and in 1 active burrow on the south fork of the lake. Traps were initially placed in only the largest and most active appearing burrows. Poor success in the first phase prompted the eventual placement of traps in many of the apparently active burrows within and in the vicinity of Study Areas 1 and 2.

Traps were placed in runways leading to burrow openings. One end of the lower section was placed in or immediately in front of, the openings. In many instances it was necessary to shape both the opening and runways to accommodate the trap. Since traps were top-heavy placement of diagonal props, secured in the mud, on both sides of the trap was necessary. Traps were covered with black plastic sacks and a mixture of mud and vegetation to decrease their visibility from the shoreline. These coverings also provided an approximate simulation of the burrow environment.

Captured animals were observed and photographed in the upper handling cage. The handling cage was then secured to the access door in the end of the holding chamber.

After the animal had entered the handling cage the sliding door was dropped and secured. The moveable curved lid was then gently pressed down on the back of the muskrat. After being properly positioned the lid was secured by inserting the dowel t-pins through both sides of the handling cage just above the top of the curved lid.

Captured muskrats were tagged, weighed, measured and sexed. General observations and photographs were made prior to release.

The curved lid in the handling cage was positioned so as to allow free access to the immobilized muskrat's ears. A 3 mm monel fingerling tag was attached at the posterior base of both ears (Aldous 1946).

After being removed from the live trap a loop of nylon seine twine was secured to the muskrat's tail. This loop was then attached to the hook on the base of a 3 kg capacity spring scale.

Approximate tail and body lengths were measured by holding the muskrat by the tip of the tail and suspending the animal next to a 3.2 cm X 1.5 m shovel handle pushed into the ground. To obtain a relatively accurate measurement it was necessary to position the muskrat so as to allow its front feet to just touch the ground. The tail tip to ground length was then marked on the rod for future measurement. A steel tape placed ventrally to the tail on the suspended animal supplied the tail length measurement.

Sexing was accomplished by palpation of the genital area in adults (Baumgärtner and Bellrose 1943) and observation of the region just anterior to the perineum for subadults (Dozier 1942).

General condition of the animal and its approximate age class were noted. Animals were released within 1 m of their capture points.

Vegetation Sampling

For descriptive and comparative purposes, vegetational data were obtained for 138 terrestrial and 160 aquatic strips (1.4 X 100 cm) at 5 m intervals near the water line in the 3 study areas. Type collections of plants occurring within 10 m of the shore line were made before and during the shoreline vegetational inspection. Dominant plants beyond the 10 m zone were identified and their distributions were recorded.

Terrestrial strips were located on a parallel line 1 m from the shore. The steel tape was supported 1 to 2 cm above the ground by 2 (9 gauge) wire supports attached to the end of the tape and pushed into the ground. Any plant stem, group of multiple stems arising from 1 visible root clump or a single rosette, was considered to be 1 plant. One-half or more of each plant 2.8 cm in diameter had to occur within the strip to be counted. Plants larger than 2.8 cm in diameter had to occur on both sides as well as within the sample area to be counted. It was necessary in 1 instance, (annual brome), to assign relative densities (sparse, medium and high) because of small stem size and high densities.

Aquatic strips were located on a line paralleling the shore in water 1 m deep. The 2 m tape was supported at or just below the water by 2 stakes tied to its ends. All floating leaved or emergent macrophytes occurring beneath or crossing over the strip were counted. In some instances this count was modified by tracing the stems to the parent plant. Multiple stems from the same plant occurring within the strip were counted as 1 plant. Shoots from colonial plants were considered to be separate plants.

A type collection of the dominant plants occurring within 10 m of the shoreline was made in each of the 3 study areas. These plants were tentatively identified, pressed and dried for purposes of final identification in the laboratory. The type collection was used for reference during the strip plant sampling procedure.

Analysis

In the analysis of external and internal data applying to each burrow, 59 variables were considered. For most of the analysis, each burrow was considered to be a separate entity with 1 mean value for each variable. A second approach involved the consideration of each observation of the variables as separate entities.

Programs used in this analysis were part of the SAS 76 system developed by the SAS Institute Inc., Raleigh North Carolina. The programs used included MEANS, CORR, FREQ, SCATTER and CLUSTER (Barr 1976).

The procedure MEANS calculates simple descriptive statistics for numeric variables. This procedure was used to build a data set that included a single mean value per burrow for all variables with more than 1 observation per burrow and to obtain the descriptive statistics for the variables.

The CORR program was used to compute Pearson's product-moment correlation coefficients between every pair of burrow variables. The RANK option provided a print of the correlation coefficients, listed in descending order, of each burrow variable and all other variables.

The FREQ procedure was used to produce one-way and two-way frequency and cross tabulation tables for burrow variables both in the mean and separate entity modes.

The SCATTER procedure was used to plot all significant correlations obtained from the CORR program. Positional plots were made using the data set containing all values of all variables.

The CLUSTER program performs a heirarchical cluster analysis. This procedure forms 1 cluster for each observation. The 2 most similar clusters are then combined. This combining of similar clusters continues until the requested number of clusters is attained.

The CLUSTER program provides, in tabular form, the maximum distance between members of a cluster, the number of distances within each of the clustering groups, the total number of distances less than the maximum diameter and a cluster map. This operation also prints, again in tabular form, the maximum average and minimum distances between and within clusters, the observations contained within the clusters and means of the variables within the clusters.

The CLUSTER procedure was used to group burrows into different numbers of clusters. During this portion of the analysis each burrow was considered to be a single unit with 1 mean value for each variable. The number of clusters and the variables included were modified to provide the most logical and useful grouping scheme.

The programs MEANS, CORR, FREQ and SCATTER were used in a stepwise fashion to describe variables, indicate relationships among variables, and to provide a condensed list of variables. This condensed variable list and the CLUSTER program were used to assign each of the burrows to a specific burrow type category. Statistical significance in all tests was determined by $\alpha = 0.05$.

RESULTS AND DISCUSSION

Activity Patterns

Shorelines occupied by burrowing muskrats in the Branched Oak Lake Research Area showed a descreasing amount of feeding activity from September to November 1976. This decrease in shoreline activity was paralleled by an increase in the utilization of marshes along the west and east shores of the north fork and the marsh along the south shore of the south fork (Fig. 11). During the first week of September all beds of cattails and arrowheads showed some signs of feeding activity as evidenced by 10 to 15 cm long stem clippings and floating tubers and roots. As September passed a distinct localization of shoreline feeding took place. Aquatic emergent beds began to brown and die back. This period was marked by intense feeding on

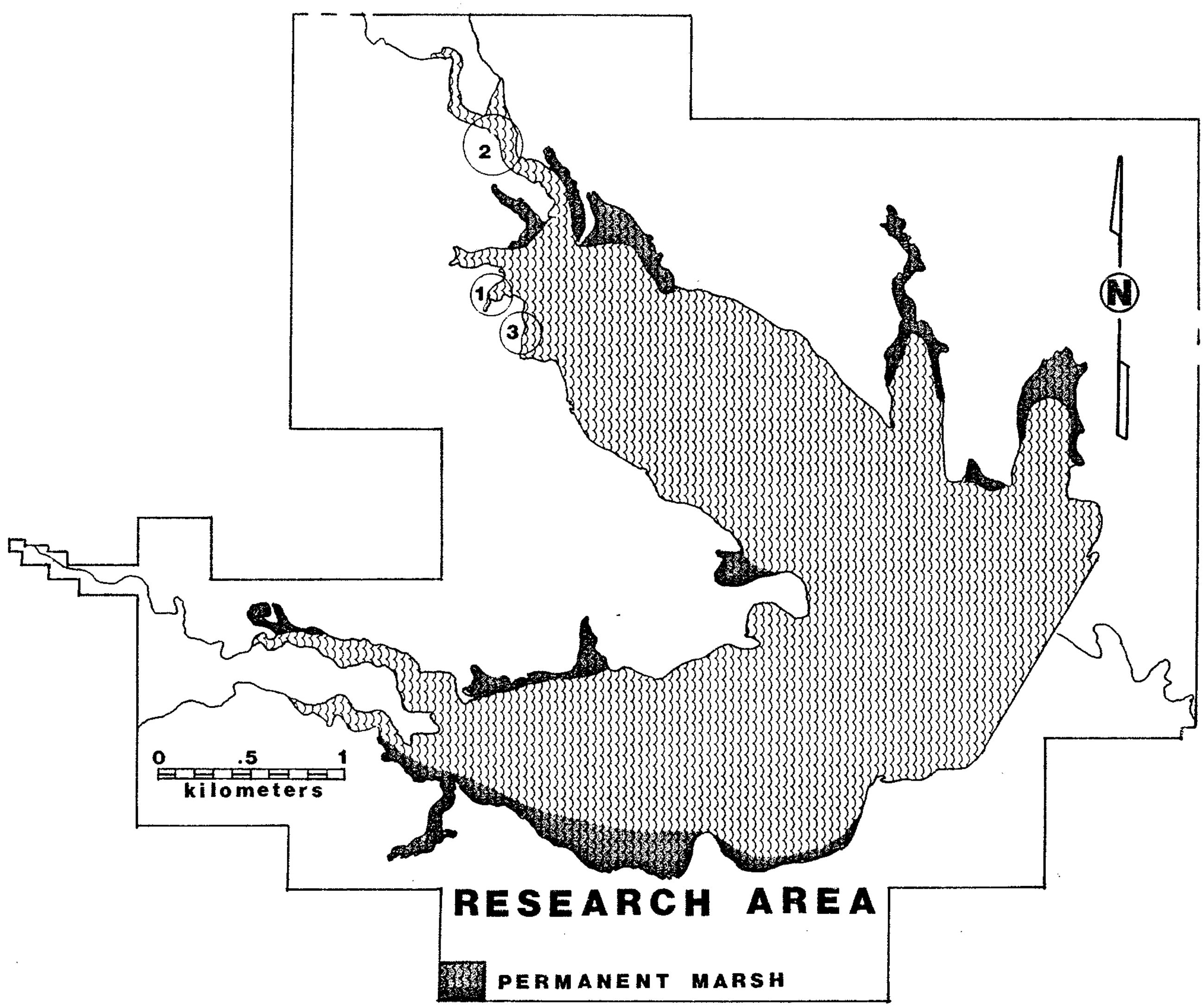

Figure 11. Marshes in the Research Area.

roots and tubers of cattails and arrowheads located within and immediately adjacent to areas that formerly showed the highest levels of utilization by muskrats. The peripheral beds of emergent aquatics showed little or no usage during this period.

By the second week in September a dramatic increase in the building and feeding activities in cattail marshes became apparent. New and renovated lodges, newly cleared open areas and rafts composed of roots and stems of cattails appeared in marshes. Prior to this time the only activity evident was limited feeding on the shoreward edges of marshes and occupancy of the largest lodges located within the densest sections of dead timber along the western boundary of the marsh along the north shore.

By 8 November 1976 visible activity of the remaining bank burrowing muskrats consisted of limited trips in the vicinity of what appeared to be their home burrows. Field examination of 3 muskrat carcasses found in Study Area 2 during this period suggested an occurrence of Errington's or Tizzer's disease (Ganaway et al. 1971, Chalmers and MacNeill 1977). The marsh dwelling segment of the population showed a slightly elevated level of feeding, raft building and lodge maintenance.

Observable muskrat activity during November 1976 through February 1977 consisted of cattail and arrowhead pieces floating just beneath the ice in Study Areas 1 and 2 and along the northern end of Study Area 3. Evidence of activity in marshes adjoining Study Area 2 was provided by concentrations of fed upon plant material floating beneath the ice in the vicinity of lodges and in specific regions that appeared to be favored feeding areas. In certain areas of the marsh another indicator of activity was bubbles frozen in ice over heavily used runways.

A single muskrat was sighted on the upstream end of Study Area 2 during March through April 1977. All study areas showed a non-typical (Errington 1963) low level of activity during this period. At the same time, although most marsh lodges were rapidly disintegrating, muskrats were frequently seen sunning themselves on most lodges and floating logs within the marshes.

The remainder of the study period (May through 13 November 1977) showed gradually increasing then decreasing levels of activity in all study areas. This same period was marked by abandonment of most marsh lodges. By July only 3 maintained lodges remained within the marsh. Feeding activity was confined to the immediate vicinity of the lodges and to the marsh border adjoining Study Area 2. Renovation of old lodges, building of new lodges and feeding within the main body of the marsh did not resume till the last week in September.

By June several logs in the downstream half of Study Area 2 were used on a regular basis as defecation points. By July free swimming muskrats were observed in all study areas. Digging activity, trails and food scraps were regularly observed.

During May arrowhead and cattails seemed to form the majority of the diet, as evidenced by stem clippings. During August and September recognizable, fed upon scraps of water hemlock, ragweed and sunflower were frequently observed floating in Study Areas 1 and 2. At the same time a shift from the typical diet of arrowhead parts to a diet of small cottonwood and willow saplings became obvious in Study Area 3. This shift coincided with a dieback exhibited by limited stands of arrowheads with this study area.

The September - November period showed a reduction in visible activity within the study areas and a parallel increase in the occupation and utilization of adjoining marsh areas. During this period roots and tubers of cattails and arrowheads were the dominant sign of muskrat feeding activity.

Burrow Excavation

STUDY AREA 1--Location, typing and excavation began at burrow 1 on the east end of the north bank of Study Area 1. Between 6 July and 3 August 1977, 29 burrows were categorized, excavated and measured.

Preliminary typing, using Earhart's criteria, indicated that of the 29 burrows, 10 were feeding burrows, 14 were winter burrows and 5 were breeding burrows.

Burrows were located on 5 separate inspection trips by visual (used twice), foot probe, hand probe and combination methods. During the first visual inspection 12 burrows, at or near water line, were located. During the second visual inspection no additional burrows were located. The foot probe inspection resulted in location of 8 new burrows. Following this hand probing uncovered 6 additional burrows. All location techniques, with the exception of probing with the iron rod, were used on the fifth inspection during which 3 more burrows were located. The efficacy of all location methods, with the exception of the visual, were affected by deep water (1.5 m) occurring within 1 m of the shoreline between 40 m and 175 m west of burrow 1.

Burrows 2-4, 7, 9, 14, 20, 22 and 29 (Fig. 8) showed evidence of recent activity. The dominant indications of activity were short pieces of clipped arrowhead stems, tracks, claw marks and disturbed earth within and in the immediate vicinity of the borrows ($\pm$ 0.5 m). Collapsed roofs and general degradation of openings were considered to be reliable indications of inactivity.

Initial observations indicated a high incidence of utilization of the substrate beneath tree root systems and dead logs, beaver dens and banks with small springs as burrowing areas by muskrats. Of the 29 burrows in Study Area 1, 6 were located beneath tree root systems or logs, 2 in the walls of inactive beaver dens and 3 contained small flowing springs.

STUDY AREA 2--Location, typing and excavation began at burrow 30 on the east end of the south bank of Study Area 2. Between 4 August and 26 September, 30 burrows were categorized and excavated.

Preliminary typing indicated that of the 30 burrows, 10 were feeding burrows, 13 were winter burrows and 7 were breeding burrows. In a few instances the extent of burrow systems was determined by proving the substrate with an iron rod.

The visual inspection, foot probe and combination methods were used on 3 inspection trips. The first or visual technique, resulted in discovery of 1 additional burrow. Heavy stands of arrowheads and reed canary grass greatly decreased efficiency of the visual inspection procedure. Because of the gradually sloping nature of the water covered substrate, foot traffic resulted in the collapse of several tunnel roofs. These tunnels were then traced to their openings.

Burrows, 30-36, 39-41, 43, 49, 50, 57 and 59 (Fig. 9) were considered active or recently active. Sightings and captures, fresh digging, tracks, food scraps and droppings were observed indicators of activity.

Burrow distribution, with respect to physical anomalies, followed much the same pattern as that in Study Area 1. Of 30 burrow systems, 12 were constructed beneath, wholly or in part, tree root systems, logs or sheets of American elm bark. The major portion of burrows 30 and 32 and all of burrow 31 were located beneath extremely dense stands of stinging nettles. The mat-like, deeply penetrating root systems of nettle may be analogous to tree root systems in their functional attraction to muskrats.

Structural differences within burrow systems, represented only in Study Area 2, included tunnel plugs and nests. Plugs, consisting of a mixture of soil and vegetative matter, were found in burrows 30, 32 and 48. These plugs were located between sections of systems used by muskrats and those used by mink. In burrow 30 the western most third of the system was effectively separated from the rest of the burrow by a series of plugged tunnels.

Burrows 30, 32 and 59 included at least 1 definable nest. The nests in the upper chambers of burrows 30 and 32 were composed of layers dominated by wadded reed canary grass, brome grass, and fragments of smartweed. In nests located in burrow 32, 3 distinct layers, varying only in state of decomposition, were discernible. The nest in burrow 30 was dominated by brome grass, reed canary grass and smartweed in a single layer. Burrow 59 had a single nest located within the highest chamber. Material in this nest was dominated by shredded polypropylene bailing twine and irregular pieces of black plastic sheet 2 to 4 cm in diameter.

STUDY AREA 3--Location, typing and excavation began at burrow 60 on the north end of Study Area 3. Between 22 September and 24 October, 26 burrows were categorized and examined.

Initial typing indicated that of the 26 burrows in Study Area 3, 20 were feeding burrows and 6 were winter burrows. In all but 4 instances it was possible to tentatively classify burrows by viewing from the burrow opening. The rest were classified by proving by hand or a branch.

The visual inspection and combination methods were used, respectively, on 2 inspection trips. Visual inspection provided the location of 24 burrows and subsequent investigation utilizing a combination of all methods, except probing with an iron rod, discovered 2 new burrows. Effectiveness of the visual location method was enhanced by the light colored bottom and lack of below water burrow openings. Difficulty in location of the last 2 burrows was related to their being obscured by a dense growth of overhanging grass.

Burrows 60, 61, 64, 68, 70, 72, 73, 80 and 82-85 (Fig. 10) showed evidence of recent activity. Indications of activity consisted of arrowhead, cottonwood, willow and cattail food scraps in and adjacent to burrows. Isolated instances of discernible digging activity was observed within some burrows.

As in other study areas many of the burrows in Study Area 3 were located beneath tree roots or logs. Of 26 burrows, 14 were beneath tree root systems or logs. Remaining burrows were located beneath heavily rooted grass that occurred in patches within the study area.

Mean Comparisons

Mean comparisons using Duncan's multiple range test were made for the 34 external and internal variables. STYP and SSLOP were the 2 classes used in mean comparisons. Results of these mean comparisons were used as an aid in selection of key variables utilized to classify muskrat burrows (Table 4).

Mean values of external and internal burrow variables were tested for significant differences among loam, clay and sand STYP and among 8 SSLOP classes. SSLOP class boundaries, in degrees, 0<10, 10<20, 20<30, 30<40, 40<50, 50<60, 60<70 and 70<80. All comparisons are listed from smallest to largest means of the variable discussed.

BSLOP--The mean comparison procedure indicated a difference among the 0 and the 30, 50, 40, and 60 SSLOP classes. This set of significant mean comparisons indicated a depressive influence exerted on burrow slopes by soil slopes measuring less than 10 degrees.

SSLOP--The single significant soil slope comparison was between $\overline{\text{SSLOP}}$ of loam and clay soil types. This significance was a reflection of the relatively high stability, lack of flood plain development and subsequent abrupt nature of banks, characteristic of clay areas inhabited by muskrats.

NOP--$\overline{\text{NOP}}$ was significantly different for the 70, 60, 40, 30, 50

Table 4. Definitions of variables used in this study.

Variable	Definition	Variable	Definition
MAREA	The Area.	CAACANT	Acanthaceae
STYP	Soil type.	CAALISM	Alismataceae
BSLOP	Burrow slope.	CACAESA	Caesalpiniaceae
SSLOP	Soil slope	CACHENO	Chenopiaceae
NOP	Number of openings.	CACOMPO	Compositae
WOP	Width of openings.	CAGRAMI	Graminae
TOP	Type of openings.	CALABIA	Labiatae
DWS	Distance to nearest opening Within burrow system.	CANAJAD	Najadaceae
		CAPOLYG	Polygonaceae
DNEXTB	Distance to nearest opening in nearest burrow system.	CAROSAC	Rosaceae
NT	Number of tunnels.	CATREES	Oleaceae, Salicaceae and Ulmaceae
WT	Width of tunnels.		
LT	Length of tunnels	CAURTIC	Urticaceae
TT	Type of tunnels.	CNOSPEC	Number of plant species.
NCHMB	Number of chambers.		
WCHMB	Width of chambers.		
LCHMB	Length of chambers.		
PEN	Bank penetration by burrow system.		
OVBRDN	Soil thickness above chamber.		
CHTW	Chamber height above the water level.		
NOBS	Number of observations per burrow.		

and 20 SSLOP classes and the 10 class. Means were also different for 70, 60, 40 and 30 classes and the 0 and 10 classes. The 0 and 10 classes were dominated by complex burrows with 3 or more openings. This indicated a locational preference for soil slopes of less than 20 degrees for construction of elaborate burrow systems.

WOP and HOP--Both WOP and HOP were significantly less for loam versus clay and loam versus sand comparisons. These significant differences were a partial result of the higher proportion of complex burrows located in areas with loam substrate. These complex burrows had characteristically small opening heights and widths.

TOP--Burrows in SSLOP classes, 70, 60, 40 and 30 had only vertical openings, many of those in the 10 class had both vertical and horizontal openings. This caused a significant difference in $\overline{\text{TOP}}$ values. This set of significant differences was a further indicator of the role soil slopes measuring less than 30 degrees played in the location of elaborate burrow complexes. All burrows with 3 or more openings had both vertical and horizontal openings. Only 3 of the burrows with 2 or fewer openings had both types of openings.

DWS--DWS means were separated into 2 significantly different categories by the mean comparison procedure. The first contained burrows in slopes within the 70, 60, 40, 20, 30 and 50 SSLOP classes. The second contained burrows in the 10 and 0 SSLOP classes. Although not all burrows in the 10 and 0 classes were complex, the 2 most complex systems were in these classes. This suggested that DWS was a valid indicator of burrow complexity.

WT and LT--$\overline{\text{WT}}$ in sand was significantly different from $\overline{\text{WT}}$ in clay and loam. $\overline{\text{LT}}$ in sand was significantly different from that in clay and loam. The primary cause of these significant differences was the many burrow systems without tunnels in areas of sand substrate. Additional causative agents that might influence width and length of tunnels were the isolated and limited distribution of reinforcing grass root clumps in sand areas and instability of sand.

TT--Tunnels in those burrows occurring in banks falling within the 70, 60, 40, 30, 20 and 50 SSLOP classes were perpendicular and/or parallel to the shoreline. These were considered to be significantly different from burrows in the 0 and 10 SSLOP classes.

Burrows in slope classes 0 and 10 included systems having all 3 tunnel types. The usual perpendicular tunnels were connected by both parallel and diagonal tunnels. Thus, TT values of 3 were another indicator of complexity.

NCHMB--The 70, 60, 40, 50, 30, 20 and 10 SSLOP class means were significantly different from the 0 class. Again the large number of internal structures characteristic of the extensive burrow in the 0 class caused a significant difference in the means.

WCHMB and LCHMB--A significant difference was noted among $\overline{\text{WCHMB}}$ in loam and those in sand and clay. The smaller sized interior chambers within the more complicated burrow systems constructed in loam contributed to this result.

$\overline{\text{LCHMB}}$ in clay was more than $\overline{\text{LCHMB}}$ in loam and sand. No reason for this significant comparison was apparent.

PEN--PEN of banks by burrow systems in slope classes 60, 40 and 50 were significantly different from those in the 10 and 0 classes. The ranges of means of classes 60, 40, 50, 20 and 30 were significantly different from that of the 0 class. The characteristic extreme values exhibited by the elaborate burrows influenced these results. A problem arose in that many of the intermediate burrows had extremely variable PEN values. This did not detract from this variable's value as an indicator of complexity.

OVBRDN--The greater $\overline{\text{OVBRDN}}$ of burrows in clay as opposed to those in loam and sand was a direct result of the abrupt soil slope that characterized most occurrences of clay substrate within the areas. Apparently muskrats responded in a restricted fashion to increasing bank height by increasing the slope of its burrow. Any bank height beyond that necessary to contain the maximum BSLOP was translated into increasing OVBRDN.

The separation of $\overline{\text{OVBRDN}}$ values in the 40, 20, 10, 30, 0, 50 and 60 classes from the 70 slope classes indicated difficulty in interpretation of mean differences when outliers were included in this type of analysis. $\overline{\text{OVBRDN}}$ of the 70 class was 1.8 m. The next largest $\overline{\text{OVBRDN}}$ (0.515 m) occurred in the 60 degree class.

CHTW--The significant differences among CHTW values for burrows in the 0 SSLOP class and those in the 40 and 50 classes denoted the relationship that CHTW had with SSLOP. It would not be unreasonable to assume that a SSLOP value of less than 10 would inhibit CHTW values. $\overline{\text{PEN}}$ comparisons suggest that when CHTW values are restricted by small SSLOP values, muskrats will respond by increasing the penetration of the bank by their burrow systems.

Means for 13 plant variables were tested for significant differences among 3 STYP and 8 SSLOP categories. These comparisons yielded 9 significant relationships of which 4 were considered to be relevant.

CAALISM--$\overline{\text{CAALISM}}$ in loam was greater than that in sand. This significant difference was an indication of a distributional pattern that was possibly a result of higher nutrient availability in loam. Another possible influence was the relative stability of the gradually sloping substrate of many loam areas as contrasted with instability of sand slopes.

CAGRAMI--Occurrence of CAGRAMI was significantly less in sand than in clay and loam. Scarcity of grass in areas of sand substrate was an obvious reflection of instability of this soil type when exposed to wave action. Erosion of upper slopes further impeded colonization of the area by most grasses. This lack of a reinforcing root mat impeded development of any but the simplest burrows.

CATREES--The 70, 60, 20, 40, 50 and 30 SSLOP class means were significantly different from the 10 class mean. Although trees were seemingly dispersed at random throughout the 3 areas, more occurred within 1 m of the water line on banks with 70 degree or greater slopes. The lack of a significant difference in $\overline{\text{CATREES}}$ values among STYPs indicates that reinforcing of the substrate by tree root systems might have increased the suitability of sand as a burrowing medium.

CNOSPEC--$\overline{\text{CNOSPEC}}$ was significantly different for sand versus clay and sand versus loam comparisons. The smaller number of species in sand can be partially explained by the relative infertility and unstable nature of the growing medium. Lack of a significant difference between $\overline{\text{CNOSPEC}}$ in clay and $\overline{\text{CNOSPEC}}$ in loam was apparently a consequence of seasonally favorable growing conditions within loam areas countered by the high relative stability of clay substrate.

Correlations

The CORR program was used to compute Pearson's product moment correlation coefficients and their associated probabilities among all possible pairs of the 34 external and internal burrow variables (Appendix 1). Correlates are listed in 2 groups in order of descending absolute values of their coefficients. This procedure was used to select variables for inclusion in the burrow typing process. This procedure was also used to detect interrelationships between internal and external measures of complexity.

STYP--WOP, WCHMB, HOP, LT AND SSLOP were significantly correlated with STYP. It was evident that lack of cohesiveness in sand would promote larger dimensions of the first 3 internal structures through the scaling off of their inside surfaces. The positive natures of the above were also influenced by the large dimensions of internal structures that were a characteristic of many of the simpler burrows that dominated areas of clay and by small values of WOP, WCHMB AND HOP that were characteristic of more complicated burrow systems that dominated loam areas.

The positive value of the STYP-SSLOP correlation coefficient was indicative of the gradually sloping banks in loam, abrupt banks of clay areas and extreme abruptness of the footslope material in sand areas.

The negative coefficient between LT and STYP likely was a result of the lack of evenly distributed root mats to counter balance the looseness of sand, a resistance of clay to digging that would partially counter its stability and evenly distributed root mats and moderate cohesiveness of loam.

Indications of plant group soil types were provided by the significant correlation coefficients between STYP and 5 plant variables.

Negative correlations among STYP and CAALISM, CAGRAMI and CNOSPEC provided information as to the high value of loam and low value of sand as growing mediums for plants represented by CAALISM and CAGRAMI. The negative correlation between STYP and CNOSPEC illustrated higher diversity of plant communities existing on loam substrates.

SSLOP--A positive relationship betweel SSLOP and BSLOP and SSLOP and CHTW suggests an active, positive response by muskrats to increasing substrate slope. This response took the form of increasing BSLOP and a greater CHTW. The positive relationship between SSLOP and OVBRDN suggests a maximum response to increasing SSLOP beyond which increases in height of burrowing medium were translated into increasing soil thickness above the chambers.

The negative correlates of SSLOP were PEN, LT, DWS, NT, NOP, NCHMB, TT and TOP. All of the negatively correlated variables with SSLOP were measures of burrow complexity. Consequently the above negative correlations indicated that SSLOP was inversely related to burrow complexity.

Lack of trees on steep slopes at burrow sites indicated by the negative SSLOP and CATREES correlation coefficient indicated that the lack of stability on steeper slopes might inhibit growth of trees.

NOP--NOP was positively correlated with NT, NCHMB, TT, PEN, LT, TOP, DWS, CHTW, DNEXTB and WT. The single negative correlation occurred between NOP and SSLOP.

The positive correlates with NOP pointed out several important relationships. The first and most obvious was the link between the number and complexity of external structures and a parallel number and complexity of internal structures. The second was the covariance between NOP, DWS and DNEXTB indicating that as the number of openings in a system increased the distance between openings and the distance between burrow systems also increased.

TOP--Positive correlation coefficients occurred among TOP and NOP, TT, DWS, NT, LT, NCHBM, PEN, WT and CHTW. TOP was negatively correlated with SSLOP.

The first 7 positive correlates were measures of burrow complexity that emphasized the importance of TOP as an indicator of increasing levels of burrow development. The correlation between TOP and WT might be spurious, caused by the significant correlation of TOP and SSLOP, and SSLOP and WT. The relationship between TOP and CHRW was a result of the strong link between the occurrence of both opening types, high CHTW values and complex burrows.

The positive relationship between WOP and HOP, and WOP and STYP was associated with the unstable nature of the sand substrate. Over time walls and roofs of openings in sand would enlarge, through the agencies of water erosion and frost action, to a much greater degree than openings in loam and clay substrates.

High values of LT and WT were positively correlated with increasing burrow complexity as opposed to the negative relationship exhibited by WOP and increasing burrow complexity. This would be a direct cause of the negative relationship between WOP and LT, and WOP and WT.

HOP--Positive correlates of HOP were WOP, OVBRDN and STYP. HOP was negatively correlated with CHTW. The confounding effects of the positive correlations of OVBRDN and STYP and the positive correlations of HOP and STYP might cause the positive correlation between HOP and OVBRDN or both might represent a response to the instability of sand. If scaling of the overhead surfaces was the reason for increased HOP in sand then a likely response would be to place burrows in the slightly more compacted layers of sand beneath the surface layer as suggested by the positive correlation between HOP and OVBRDN. If this is true then it would follow that CHTW would be less as indicated by the negative relationship between HOP and CHTW.

DWS--The variables TT, TOP, LT, NOP, NT, NCHMB, PEN and WT were positively correlated with DWS. The correlation between DWS and SSLOP was negative.

The positive correlations provided strong evidence for the role that DWS played as an external sign of burrow complexity. Although the relationships between the variables were clear, reasons for the positive correlation with DWS were not. There seemed no readily apparent explanation for the greater distance between adjacent openings within extensive burrow systems. A possible cause, in some instances, might be a response to obstructions (tree root systems) or small scale topographic changes in the substrate that would have more of an effect on burrows that covered large areas.

DNEXTB--The variates PEN, NOP, CHTW, TT, NT and NCHMB were positively linked to DNEXTB.

As with DWS the positive correlates of DNEXTB were all strong indicators of burrow complexity. The most elaborate burrows contributed most to the maximization of DNEXTB. These gaps between burrows, observed by others (Johnson 1925, Earhart 1969) might be related to territorial boundaries perceived and defended by residents. Possible explanations for the decreasing distance between less complex burrows might be that they served as satellite refuges or that most served as community feeding structures and therefore were not rigidly defended.

LT, TT and NT--NT was positively correlated with NCHMB, NOP, PEN, TT, LT, DWS, TOP, CHTW, WT and DNEXTB. The single negative correlation occurred between NT and SSLOP.

TT was positively correlated with NOP, NT, PEN, NCHMB, DWS, TOP, LT, WT, DNEXTB and CHTW. TT was negatively correlated with SSLOP.

LT was positively correlated with PEN, NT, NOP, NCHMB, TT, DWS, WT, TOP and negatively correlated with SSLOP, WOP and STYP.

The positive correlates of NT, TT and LT served to emphasize the close relationship of internal structures with detectable external variables.

The negative coefficient of LT and WOP pointed out the tendancy for large values of the tunnel variables and small values of WOP being associated with higher levels of development in burrow systems.

The unstable nature of sand and resistance to digging in clay promoted the negative relationship shown by LT and STYP correlation coefficients.

NCHMB, WCHMB and LCHMB--NCHMB was positively correlated with NT, NOP, PEN, TT, LT, DWS, TOP, CHTW, DNEXTB and WT. NCHMB was negatively correlated with SSLOP. Positive correlates of WCHMB were LCHMB and STYP. LCHMB was positively correlated with WCHMB.

The above series of positive correlations indicated that WCHMB and LCHMB were independent of the varying levels of complexity. This independence plus the differential use of burrow types suggested that chamber size and function were not interrelated and therefore of little value in a burrow typing procedure.

PEN--PEN was positively correlated with LT, NT, NCHMB, NOP, TT, DWS, WT, TOP DNEXTB and CHTW, and negatively correlated with SSLOP. The strong covariance, both positive and negative, among measures of burrow complexity was previously defined, the exception being the positive relationship between PEN and CHTW. It was obvious that as a burrow was extended farther into the bank that chambers contained in that burrow would, in most instances, be farther above the water.

OVBRDN--The positive relationship between OVBRDN and HOP might reflect a response by muskrats to increased height of digging medium available. Because of limitations on the positive relationship between OVBRDN and BSLOP it would be reasonable to suggest that once the limit was reached a higher level of SSLOP would simply result in thicker soil cover above the chambers.

CHTW--CHTW was positively correlated with BSLOP, NOP, NCHMB, NT, PEN, SSLOP, DNEXTB, TT and TOP. A negative correlation occurred between CHTW and HOP.

The positive correlates again served as indicators of the importance CHTW played in the classification of burrow types. The negative relationship between CHTW and HOP suggested a relationship between larger openings and less complicated burrow types. This was partially supported by the correlations already described.

CAALISM and CACOMPO--The negative correlates of CAALISM (STYP, WOP, CACOMPO, HOP) and the negative correlates of CACOMPO (CAALISM, DWS, LCHMB, WCHMB, TOP, TT) indicated that these 2 variables were positively and negatively associated, respectively, with increasing levels of complexity of burrow systems. This effect was in part due to the confounding influence of STYP. Within the 3 areas these plants were indicators of the conditions influencing burrow complexity and in the case of CAALISM a positive locational preference may have been indicated.

CAGRAMI--CAGRAMI was negatively associated with STYP. This indicated the higher suitability of loam and the lower suitability of sand as growing mediums. The unstable nature of sand and high susceptibility of the areas of sand substrate to erosion plus the relative infertility of sand may have been the major contributors to this correlation.

CAPOLYG--CAPOLYG was positively associated with TOP, NOP and TT all of which were very definite indicators of burrow complexity. The plants represented by CAPOLYG were utilized both as food and nesting material. Another contributing factor may have been the persistent nature of root mats formed by members of CAPOLYG.

CATREES--CATREES was negatively correlated with CHTW, SSLOP and BSLOP and positively correlated with TOP and CAALISM. These relationships suggested positive association between CATREES and those conditions favoring burrow complexity.

CNOSPEC--CNOSPEC was negatively correlated with CHTW, SSLOP and BSLOP and positively correlated with STYP and DNEXTB. The positive correlates served as indicators of plant diversity. The negative correlates suggested that there was an inverse relationship between CNOSPEC and increasing burrow complexity.

Clustering

A hierarchal clustering procedure (Barr 1976) was used to separate the 85 burrows excavated into 9 types, based on measures of similarity among observations and groups of observations.

This agglomerative strategy proceeds by progressive fusion of single member clusters, representing individual observations, and ceases when there is a single cluster representing the whole population. This polythetic system measures the similarity of the attributes of each cluster and then combines it with another cluster with which, on the average, it is most similar to (Fig. 12) (Williams 1971).

The 59 variables measured in the excavation portion of this study were selected with the intention of quantifying burrow dimensional and distributional characteristics. A series of clustering operations based on various combinations of most of these variables provided a series of groups with indefinite intergroup boundaries. The results of this portion of the clustering procedure provided information as to the overall similarity of burrows and little else. The complexity of these results prevented their utilization for infield separation of burrows, the major objective of this study.

Efforts to discern the most concise but descriptive group of variables needed for the formation of a classification scheme, began with the computation of Pearson's product moment correlation coefficients, frequency tables and the testing of significant differences among the means of STYP and SSLOP classes.

These statistical procedures provided means by which a secondary attribute list was selected. This list contained 34 variables used throughout the intermediate phases of this study.

Clustering separations utilizing variables contained in the secondary list again provided indications of patterns and suggestions as to variables having the most influence on intercluster boundaries.

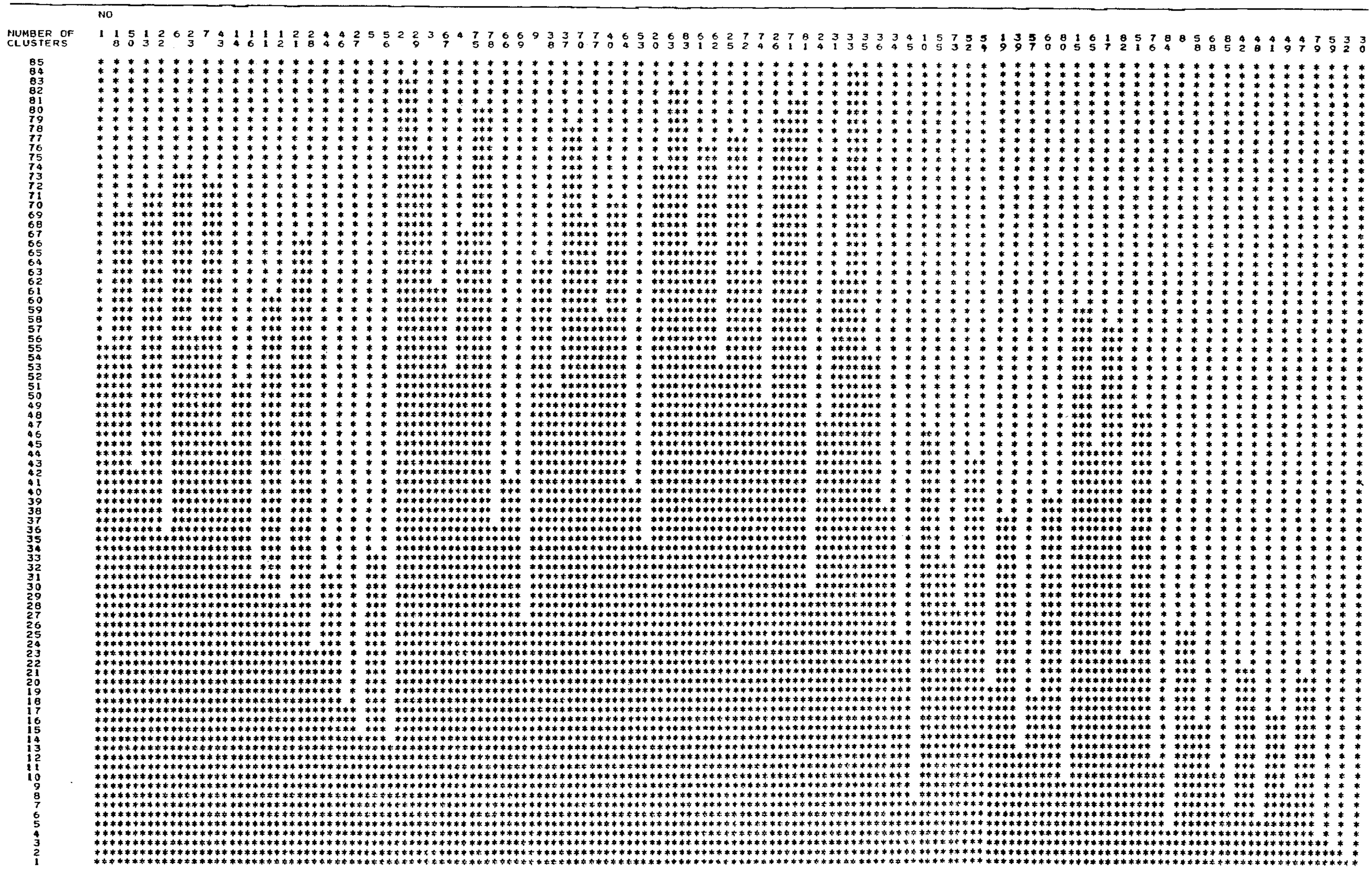

Figure 12. Cluster map illustrating the agglomerative fusion of observations and groups of observations representing muskrat burrows.

This intermediate list contained quantifiable and qualifiable dimensional burrow variables and 13 plant variables. Correlations were reviewed and variables not externally measureable or only weakly indicative of patterns were eliminated. Those eliminated included all plant variables and many of the quantifiable dimensional variables. As mentioned before this procedure was aimed at providing a tentative classification system for muskrat burrows that could be readily utilizied for management purposes. In some instances this aim obviously influenced the choice of variables included in the cluster analysis. But with this type of procedure it was necessary to make subjective decisions and not to entirely rely on a numerical solution (Williams 1971).

The tertiary variable list contained the following; NOP, TOP, DWS, NT, TT, NCHMB, PEN, and CHTW. These variables allowed the segregation of the 85 burrows into acceptably homogeneous types (Table 5).

The optimum number of burrow types was indicated by the lack in significant reduction in cluster diameters (Johnson 1967) (Table 6). This approach provided the smallest number of readily interpretable groups.

Burrow Types

Type I burrows (cluster 1) were strongly dominated by systems with 1 vertical opening, 0 to 1 straight tunnels and 1 chamber. These 55 burrows had a $\overline{\text{PEN}}$ of 0.395 m and a $\overline{\text{CHTW}}$ value of 0.024 m. Field observation of fresh food scraps indicated that these burrows were used as feeding structures and as possible temporary resting quarters. Determination of activity based on sign census indicated that 22 of

Table 5. Muskrat burrow types as defined by cluster groupings.

CLUSTER	NO	NOP	TOP	DWS	NT	TT	NCHMB	PEN	CHTW
1	1	1.0	1.0	0.00000	1.0	1.0	1.0	0.52000	0.06500
1	18	1.0	1.0	0.00000	1.0	1.0	1.0	0.61000	0.09500
1	50	1.0	1.0	0.00000	1.0	1.0	1.0	0.59000	0.05000
1	13	1.0	1.0	0.00000	1.0	1.0	1.0	0.46000	-0.01500
1	22	1.0	1.0	0.00000	1.0	1.0	1.0	0.50000	0.00000
1	6	1.0	1.0	0.00000	1.0	1.0	1.0	0.44000	0.13000
1	23	1.0	1.0	0.00000	1.0	1.0	1.0	0.40000	0.14000
1	7	1.0	1.0	0.00000	1.0	1.0	1.0	0.41000	0.09000
1	43	1.0	1.0	0.00000	1.0	1.0	1.0	0.42000	0.05000
1	14	1.0	1.0	0.00000	1.0	1.0	1.0	0.38000	0.20000
1	16	1.0	1.0	0.00000	1.0	1.0	1.0	0.51000	0.18000
1	11	1.0	1.0	0.00000	1.0	1.0	1.0	0.29000	-0.07500
1	12	1.0	1.0	0.00000	1.0	1.0	1.0	0.37000	-0.07500
1	21	1.0	1.0	0.00000	1.0	1.0	1.0	0.74000	0.07500
1	28	1.0	1.0	0.00000	1.0	1.0	1.0	0.81000	0.08000
1	44	1.0	1.0	0.00000	1.0	1.0	1.0	0.59000	-0.79000
1	46	1.0	1.0	0.00000	1.0	1.0	1.0	0.66000	-0.47500
1	27	1.0	1.0	0.00000	1.0	1.0	0.0	0.40000	0.00000
1	5	2.0	1.0	0.25000	1.0	1.0	1.0	0.30000	0.06500
1	56	2.0	1.0	0.19000	1.0	1.0	1.0	0.61500	0.05000
1	2	1.0	1.0	0.00000	0.0	1.0	1.0	0.47000	0.05500
1	29	1.0	1.0	0.00000	0.0	1.0	1.0	0.46000	0.05000
1	3	1.0	1.0	0.00000	0.0	1.0	1.0	0.49000	0.07000
1	67	1.0	1.0	0.00000	0.0	1.0	1.0	0.49000	-0.01000
1	4	1.0	1.0	0.00000	0.0	1.0	1.0	0.58000	0.04000
1	75	1.0	1.0	0.00000	0.0	1.0	1.0	0.53000	0.02500
1	78	1.0	1.0	0.00000	0.0	1.0	1.0	0.52000	0.04500
1	66	1.0	1.0	0.00000	0.0	1.0	1.0	0.66000	-0.07500
1	69	1.0	1.0	0.00000	0.0	1.0	1.0	0.71000	0.11000
1	9	1.0	1.0	0.00000	0.0	1.0	1.0	0.10000	-0.02000
1	38	1.0	1.0	0.00000	0.0	1.0	1.0	0.12000	0.05000
1	37	1.0	1.0	0.00000	0.0	1.0	1.0	0.22000	-0.04000
1	70	1.0	1.0	0.00000	0.0	1.0	1.0	0.23000	-0.01500
1	77	1.0	1.0	0.00000	0.0	1.0	1.0	0.21000	0.01500
1	40	1.0	1.0	0.00000	0.0	1.0	1.0	0.17000	-0.02000
1	64	1.0	1.0	0.00000	0.0	1.0	1.0	0.18000	-0.06500
1	53	1.0	1.0	0.00000	0.0	1.0	1.0	0.20000	-0.14000
1	20	1.0	1.0	0.00000	0.0	1.0	1.0	0.28000	0.05000
1	63	1.0	1.0	0.00000	0.0	1.0	1.0	0.24000	0.05000
1	83	1.0	1.0	0.00000	0.0	1.0	1.0	0.25000	0.04500
1	61	1.0	1.0	0.00000	0.0	1.0	1.0	0.26000	0.01500
1	62	1.0	1.0	0.00000	0.0	1.0	1.0	0.28500	-0.00500
1	25	1.0	1.0	0.00000	0.0	1.0	1.0	0.32000	0.09000
1	72	1.0	1.0	0.00000	0.0	1.0	1.0	0.34000	0.07000
1	74	1.0	1.0	0.00000	0.0	1.0	1.0	0.35000	0.02000
1	26	1.0	1.0	0.00000	0.0	1.0	1.0	0.26000	0.12000
1	71	1.0	1.0	0.00000	0.0	1.0	1.0	0.26000	0.10000
1	81	1.0	1.0	0.00000	0.0	1.0	1.0	0.27000	0.09500
1	24	1.0	1.0	0.00000	0.0	1.0	1.0	0.43000	0.13000
1	31	1.0	1.0	0.00000	0.0	1.0	1.0	0.35000	0.16500
1	33	1.0	1.0	0.00000	0.0	1.0	1.0	0.33000	0.24000
1	35	1.0	1.0	0.00000	0.0	1.0	1.0	0.33000	0.24000
1	36	1.0	1.0	0.00000	0.0	1.0	1.0	0.42000	0.24000
1	34	1.0	1.0	0.00000	0.0	1.0	1.0	0.24000	0.24000
1	45	1.0	1.0	0.00000	0.0	1.0	1.0	0.17000	-0.52500
1	MEAN	1.0	1.0	0.00800	0.4	1.0	1.0	0.39527	0.02355
2	10	1.0	1.0	0.00000	1.0	1.0	2.0	0.60000	-0.09000
2	55	1.0	1.0	0.00000	1.0	1.0	2.0	0.74250	-0.15000
2	73	1.0	1.0	0.00000	1.0	1.0	2.0	0.45500	-0.00500
2	52	1.0	1.0	0.00000	1.0	1.0	2.0	0.24750	-0.43500
2	54	1.0	1.0	0.00000	1.0	1.0	2.0	0.42500	-0.42000
2	19	1.0	1.0	0.00000	1.0	1.0	2.0	1.20000	0.20500
2	39	1.0	1.0	0.00000	1.0	1.0	2.0	1.31500	0.00500
2	57	2.0	1.0	0.86500	1.0	1.0	2.0	0.64500	-0.52000
2	60	2.0	1.0	0.56000	1.0	1.0	3.0	0.48167	0.03500
2	80	2.0	1.0	0.41000	1.0	1.0	3.0	0.61000	0.09667
2	15	1.0	1.0	0.00000	0.0	1.0	2.0	0.40000	0.07000
2	65	1.0	1.0	0.00000	0.0	1.0	2.0	0.40500	-0.01500
2	17	1.0	1.0	0.00000	0.0	1.0	2.0	0.29500	0.11000
2	82	1.0	1.0	0.00000	0.0	1.0	2.0	0.25500	0.03250
2	51	1.0	1.0	0.00000	0.0	1.0	3.0	0.27833	-0.10000
2	76	1.0	1.0	0.00000	0.0	1.0	3.0	0.37167	0.00500
2	84	2.0	2.0	0.25000	0.0	1.0	2.0	0.25500	0.12000
2	MEAN	1.2	1.1	0.12265	0.6	1.0	2.2	0.52833	-0.06211
3	8	2.0	1.0	0.41500	3.0	2.0	2.0	0.90000	-0.14500
3	58	2.0	1.0	0.51000	3.0	2.0	2.0	0.20750	-0.48000
3	68	2.0	1.0	0.25000	2.0	2.0	2.0	1.06750	0.01750
3	85	1.0	1.0	0.00000	2.0	2.0	1.0	0.71500	0.07000
3	MEAN	1.8	1.0	0.29375	2.5	2.0	1.8	0.72250	-0.13437
4	42	2.0	2.0	0.67000	2.0	2.0	3.0	0.93500	-0.35833
4	48	2.0	2.0	0.76000	2.0	2.0	4.0	0.66500	-0.09750
4	MEAN	2.0	2.0	0.71500	2.0	2.0	3.5	0.80000	-0.22792
5	41	3.0	2.0	0.24333	1.0	1.0	1.0	0.50000	0.05000
5	49	4.0	2.0	0.22500	1.0	1.0	2.0	0.56250	-0.08000
5	MEAN	3.5	2.0	0.23417	1.0	1.0	1.5	0.53125	-0.01500
6	47	3.0	2.0	0.41667	2.0	2.0	1.0	0.49000	0.44000
6	79	3.0	2.0	0.46667	2.0	2.0	2.0	0.64000	0.04500
6	MEAN	3.0	2.0	0.44167	2.0	2.0	1.5	0.56500	0.24250
7	59	6.0	2.0	0.28833	5.0	2.0	4.0	0.57750	0.01375
8	32	11.0	2.0	0.37182	14.0	3.0	16.0	2.09250	0.75000
9	30	14.0	2.0	0.87929	29.0	3.0	34.0	2.56618	0.59500

Table 6. Maximum cluster diameters.

NUMBER OF CLUSTERS	MAXIMUM DISTANCE WITHIN A CLUSTER	NUMBER OF DISTANCES WITHIN <= MAXIMUM	NUMBER OF DISTANCES IN ALL <= MAXIMUM	RATIO
85	0.00000000	0	1	0.00000
84	0.00000000	1	1	1.00000
83	0.00012500	2	4	0.50000
82	0.00012500	3	4	0.75000
81	0.00012500	4	4	1.00000
80	0.00050000	5	6	0.83333
79	0.00072500	7	9	0.77778
78	0.00072500	8	9	0.88889
77	0.00080000	9	10	0.90000
76	0.00102500	10	13	0.76923
75	0.00130000	12	15	0.80000
74	0.00160000	14	17	0.82353
73	0.00170000	15	21	0.71429
72	0.00170000	16	21	0.76190
71	0.00182500	17	23	0.73913
70	0.00212500	18	26	0.69231
69	0.00242500	19	28	0.67857
68	0.00312500	21	47	0.44681
67	0.00362500	23	52	0.44231
66	0.00492500	24	68	0.35294
65	0.00505000	30	70	0.42857
64	0.00530000	31	74	0.41892
63	0.00580000	33	80	0.41250
62	0.00602500	35	85	0.41176
61	0.00640000	38	88	0.43182
60	0.00640000	39	88	0.44318
59	0.00725000	40	97	0.41237
58	0.00730000	46	100	0.46000
57	0.00760625	47	103	0.45631
56	0.00850000	51	115	0.44348
55	0.00900000	53	121	0.43802
54	0.01052500	56	137	0.40876
53	0.01300000	71	158	0.44937
52	0.01450000	83	170	0.48824
51	0.01730000	84	192	0.43750
50	0.01810000	94	197	0.47716
49	0.01810000	118	197	0.59898
48	0.01973611	119	208	0.57212
47	0.02210000	123	229	0.53712
46	0.02390625	124	242	0.51240
45	0.02500000	132	255	0.51765
44	0.02772500	136	271	0.50185
43	0.03173125	137	291	0.47079
42	0.03460000	143	311	0.45981
41	0.03672500	144	318	0.45283
40	0.04250000	151	357	0.42297
39	0.04277222	152	358	0.42458
38	0.04820000	157	383	0.40992
37	0.05322500	158	407	0.38821
36	0.06609994	172	466	0.36910
35	0.06659997	202	468	0.43162
34	0.07119995	290	481	0.60291
33	0.10304999	291	561	0.51872
32	0.10368121	293	562	0.52135
31	0.10412496	294	564	0.52128
30	0.13129997	316	597	0.52931
29	0.19279999	430	652	0.65951
28	0.29442495	456	691	0.65991
27	0.32624996	462	701	0.65906
26	0.38900000	687	716	0.95950
25	0.60080624	688	739	0.93099
24	0.69482499	722	746	0.96783
23	1.02419949	752	995	0.75578
22	1.04437733	760	1133	0.67079
21	1.14903355	761	1433	0.53105
20	1.18102455	762	1468	0.51907
19	1.33315563	772	1560	0.49487
18	1.58852768	774	1636	0.47311
17	1.66019917	791	1649	0.47968
16	2.02114201	792	1761	0.44974
15	2.05470562	794	1829	0.43412
14	2.08482456	830	1884	0.44055
13	2.56474972	1530	2137	0.71596
12	3.00894356	1551	2188	0.70887
11	3.11144352	1557	2247	0.69292
10	3.82015610	1560	2331	0.66924
9	4.19932461	1630	2448	0.66585
8	4.31239223	1634	2468	0.66207
7	10.32149410	2569	3000	0.85633
6	11.60815620	2577	3108	0.82915
5	13.09638119	2601	3264	0.79688
4	20.65731812	3321	3321	1.00000
3	61.53942871	3403	3403	1.00000
2	533.56518555	3486	3486	1.00000
1	2119.81933594	3570	3570	1.00000

the Type I burrows were active.

Type II burrows (cluster 2) were dominated by systems with a single vertical opening. The majority of these 17 burrows had 0 to 1 straight tunnels and 2 to 3 chambers. These burrow systems had a $\overline{\text{PEN}}$ value of 0.528 m and $\overline{\text{CHTW}}$ value of -0.062 m. Most of these burrows could have been, at one time, seasonably suitable as both breeding (multi-chamber) and feeding structures. At the time of excavation, many of the chambers were partially or completely submerged and therefore unuseable. Observation of sign indicated that 7 of the 17 Type II burrows were active.

Of 4 Type III burrows, 3 had 2 vertical openings. $\overline{\text{DWS}}$ for these burrows was 0.294 m. These systems had 2 to 3 tunnels at least 1 of which was perpendicular and 1 parallel to the shoreline. Of 4 systems within this type, 3 had 2 chambers. $\overline{\text{PEN}}$ value for Type III burrows was 0.723 m and $\overline{\text{CHTW}}$ was -0.134 m. Two of the Type III burrows were active.

Both of the Type IV burrows had 2 openings, 1 of which was vertical, the other horizontal. $\overline{\text{DWS}}$ value for the 2 burrows was 0.715 m. Each had 1 tunnel perpendicular to the shore and 1 parallel to the shoreline. Type IV burrows had 3 to 4 chambers with a $\overline{\text{PEN}}$ value of 0.800 m and a $\overline{\text{CHTW}}$ value of -0.228 m. A nest and other recent sign indicated that 1 Type IV burrow was active.

Type V burrows had 3 to 4 openings of both types. $\overline{\text{DWS}}$ for Type V burrows was 0.234 m. Both burrows within this type had a single tunnel perpendicular to the shoreline and 1 to 2 chambers. $\overline{\text{PEN}}$ for these burrows was 0.531 m and $\overline{\text{CHTW}}$ was -0.015 m. Both Type V burrows showed signs of activity.

The Type VI burrows had 3 openings of both types. $\overline{\text{DWS}}$ value was -0.442 m. Each of the burrows of this type had 2 tunnels 1 straight and 1 perpendicular to the shoreline and 1 to 2 chambers. $\overline{\text{PEN}}$ value was 0.565 m and $\overline{\text{CHTW}}$ value was 0.243 m. Both burrows of this type were judged inactive.

The single Type VII burrow had 6 openings including both horizontal and vertical types. $\overline{\text{DWS}}$ value for Type VII burrows was 0.288 m. The burrow had 5 tunnels that included both perpendicular and parallel types. This burrow had 4 chambers, a $\overline{\text{PEN}}$ of 0.578 m and a $\overline{\text{CHTW}}$ of 0.014 m and was judged inactive.

The single Type VIII burrow had 11 openings, and included both types. $\overline{\text{DWS}}$ for this system was 0.372 m. This burrow contained 14 tunnels including those perpendicular, parallel and diagonal to the shoreline. This system contained 16 chambers and had a $\overline{\text{PEN}}$ of 2.093 m. $\overline{\text{CHTW}}$ for this system was 0.750 m. Activity within and in the vicinity of this burrow was very apparent.

The single Type IX burrow was the most extensive burrow system excavated. It contained 14 openings, including both vertical and horizontal types, and had a $\overline{\text{DWS}}$ of 0.0879 m. This complex contained 29 tunnels in a mixture of all 3 tunnel types. This complex had 34 chambers, a $\overline{\text{PEN}}$ of 2.566 m and a $\overline{\text{CHTW}}$ value of 0.595 m. Sightings during excavation and capture, and large amounts of sign indicated that this burrow was the most active of all burrows examined within the study areas.

Occupancy and Usage of Burrow Types

Absolute statements as to usage and occupancy patterns of burrow

Types I, II and III could not be made because of lack of capture-recapture information. Usage patterns were suggested, based on the dimensional information provided by this study and data provided by Earhart (1969), Beshears and Haugen (1953) (Table 6) and Errington (1963).

Type I burrows, because of their simplicity in the number and extent of internal structures, their association with banks and substrates of marginal value as burrowing mediums (Earhart 1969) and their dominant occurrence, were typified as satellite refuges. They served as both feeding structures and temporary refuges for the transient segment of the population (Shanks and Arthur 1952).

Type II and Type III burrows represented the initial steps toward permanency. Because of similarity of Type III burrows to Type II burrows it was possible that the former was a simple elaboration of the latter. Well situated burrows in the Type II category would be reoccupied and perhaps expanded when the original resident was removed (Earhart 1969). These burrows were extensive enough to protect a breeding female and 1 litter during normal water level conditions. Long term abnormally high water levels would prevent these burrows from being used.

Because of the higher number of chambers and the relatively large area encompassed by Type IV burrows it would be reasonable to suggest that they were capable of supporting 1 breeding female and possibly members of 2 successive litters. As with Type II and III burrows potential occupants of Type IV burrows were subject to forced evacuation during periods of high water. Their relatively extensive nature suggested durability. This plus Errington's (1948) statement that

Table 7. Some reported values for muskrat burrow variables.

Variable	All Burrows[1]			Feeding Burrows			Winter Burrows			Breeding Burrows[2]			All Burrows[3]		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min[a]	Max[a]
SSLOP (°)	--	--	--	34	15	45	47	14	80	39	11	80	36.2	0.1	79.6
NOP	2	1	9	1.40	1	2	1.5	1	2	4.6	2	8	1.57	1	14
DWS (m)	1.07	0.31	2.44	---	---	---	---	---	---	---	---	---	0.09	0.19	1.63
DNEXTB (m)	--	--	--	1.22	0.91	3.05	6.10	0.61	18.28	3.96	0.91	15.24	3.98	0.03	43.29
NCHMB	2	1	6	1	1	1	1.2	1	2	3.7	2	6	1.95	0	34
WCHMB (m)	0.20	0.15	0.25	---	---	---	---	---	---	---	---	---	0.19	0.08	0.55
PEN (m)	1.47	1.22	1.83	0.66	0.31	1.17	1.07	0.15	3.96	2.01	1.07	5.49	0.50	0.10	6.15
OVBRDN (m)	0.25	0.05	0.66	0.05	0.03	0.08	0.46	0.08	1.52	0.21	0.08	0.76	0.28	0.04	2.60
CHTW (m)	0.41	0.25	0.61	0.127	0.08	0.18	0.41	0.15	0.66	0.48	0.28	0.91	0.01	-0.79	0.75

1 From Beshears and Haugen (1951)

2 From Earhart (1969)

3 Partial results of this study.

a Values for all observations of the variables.

muskrats reoccupied existing burrows when conditions returned to normal indicated that these burrows were an adjunct to long term stability within muskrat populations.

Both of the Type V burrows had 3 to 4 openings leading into 1 tunnel. Both of these systems were located beneath trees. The abnormal number of openings within these 2 systems was a response to the reinforcing nature of roots. In sections of unreinforced burrowing medium, this number of openings in a comparable area would result in a very short lived burrow because of structural instability. No justification for this number of openings was apparent. In any case the structural stability provided by root structures would greatly increase the useful life of these 2 systems. As breeding burrows they were marginally suitable but might provide eminently habitable winter quarters because of the insulative value inherent in the supportive root structure. This root structure would also eliminate problems caused by the freeze-thaw cycle (Elder 1969).

Type VI burrows, although containing only 1-2 chambers, could be capable of housing 1 breeding female and 1 of her litters. These multi-opening multi-tunnel systems might represent an intermediate constructional phase in burrow excavation. The relatively high DWS value, NOP value of 3, moderate PEN value and moderate CHTW value may counter balance the simplifying effect of the limited number of chambers.

Type VI burrows could securely shelter a family of muskrats during a period of temporarily elevated water levels or soon after the water level recedes. Security of residents during and immediately after increases in water level was an important determiner of the stability of a muskrat population (Bellrose and Low 1943).

The single Type VII burrow was elaborate and extensive. The inclusion of 4 chambers and 5 tunnels with the attendant 6 openings suggested enough living space was available to shelter 1 breeding female and at least 2 of her litters during the breeding season. Again because of the extensive nature of this system, more than 1 family unit could occupy this burrow during fall and winter (MacArthur and Aleksuik 1979). Although not indicated by $\overline{\text{CHTW}}$ value, 2 of the chambers within this system did exceed the mean. Residents of this system, during a moderate rise in water level would be more secure than those within less complex systems with lower $\overline{\text{CHTW}}$ values.

The single Type VIII burrow was the first system to truly fit Errington's (1940) "population loci" concept. The 16 chambers within this complex could provide shelter during the breeding season for 1 adult female, 2 to 3 of her current season's litters and possibly some sub-adults from her previous season's litters. The lack of susceptibility of residents of this burrow complex to even large water level increases was shown by $\overline{\text{CHTW}}$ value of 0.750 m. Year round suitibility of this complex was readily apparent.

The single Type IX burrow represented the epitomy of those burrows qualifying as "ultimate" refuges (Errington 1948). The 34 chambers in this system contained members of 3 different litters of the season and 1 subadult (observed during live trapping (Appendix 2) and burrow excavation). Because of extreme complexity and extent, and presence of plugs and collapsed tunnels throughout this system it was assumed that this structure could shelter members of several families throughout the year. The high level of security of this complex was further indicated by the inclusion of an active mink den within the area of the system farthest from the water.

Management Applications

A burrow type census would begin with a review of the overall suitability rating of the substrate's quality as a burrowing medium. Sections of substrate composed of unstable, loose, coarse textured soil without supporting root structures would be eliminated. Sections of frequently inundated very gradually sloping banks would also be eliminated.

Those sections of substrate considered as suitable burrowing medium would then be determined by using a visual check for openings, a sign census and an inspection of physical anomalies attractive to muskrats. This could then be followed by a hand or foot probe inspection for concealed burrow openings.

After location of actual burrow sites, the typing procedure could then be initiated. A visual inspection from openings at or partially below water line would classify most Type I burrows. This could be followed by a hand probe inspection through the opening to check for multiple chambers (Type II) or multiple chambers and multiple tunnels serving to connect openings (Type III).

The occurrence of horizontal openings would indicate Types IV, V, VI, VII, VIII or IX burrow systems. A hand probe inspection for cross tunnel connections between openings, chamber number, and measurements between openings would serve to separate and classify Type IV and V burrows.

Probing the substrate with a metal rod with a bulbous tip was a method used by Warwick (1936) to detect burrows. This method can also be used to count and classify internal burrow structures. When pushed into the substrate, resistance is noticeable, until the rod intersects a tunnel or chamber. Repeated probing would provide counts and types of internal structures and the area covered by the system. Resistant substrates can be penetrated by pounding the rod with a hammer. Opening counts, measurements between openings, and the presence of cross tunnels would serve to isolate Type VII burrows.

The remaining burrows could be classified by visual opening counts and probing to determine the presence of diagonal tunnels and tunnel connections between openings. Measurements of distances between openings, probing counts of internal structures, and probing to determine bank penetration by the systems and chamber heights above water level would serve to segregate Type VIII and Type IX burrows from the rest of the burrows and each other.

Baseline data provided by this study could be used to measure the proportion of feeding and refuge burrows to burrows suitable, seasonably or year round, for breeding. This proportion could serve as a measure of the quality and stability of the habitat. A large ratio would indicate widely dispersed, patchy distribution of favored food sources. A low ratio would indicate long term environmental stability and readily available food sources.

A burrow type census would provide a measure of the potential supportive base for a breeding muskrat population. This burrow type census combined with burrow type occupancy patterns, sign census, and current reproductive rate would serve as a numerical indicator of burrowing muskrat population levels.

SUMMARY

The building habits of a muskrat population (*Ondatra zibethicus zibethicus*) in southeastern Nebraska were studied from 1 September 1976 to 13 November 1977. This population was intensively harvested annually and may have been affected by drought. Errington's or Tizzer's disease, as suggested by infield carcass examination and abnormal levels of scavenging (Appendix 3), may have exerted a population depressing influence.

Muskrat burrows within Branched Oak Lake Recreation Area were separable into 9 types based on number and type of burrow openings, distance between burrow openings within the system, number and type of tunnels, number of chambers, chamber height above water level and the distances burrow systems penetrated the bank.

Burrow Types I through VI were considered adjuncts to the complex burrows. These burrows were located in banks with slopes of 0 to 79.6 degrees and occurred in substrate sections of loam, clay and sand. A preference for locating burrows beneath reinforcing root systems was evident. These relatively simple burrows were characterized as seasonally available and suitable as feeding, refuge and in some cases, breeding structures. Burrow Types I through VI, in normal years, would provide shelter for a well dispersed breeding muskrat population.

Burrow Types VII through IX were found within areas of loam substrate and on slopes measuring less than 30 degrees. These burrows were within areas favoring growth of plants represented by CAALISM, CAGRAMI, CAPOLYG and CATREES. These burrows showed extreme values of most quantifiable and qualifiable dimensional variables. Measurements

and observations of these systems indicated that they were relatively immune to environmental fluctuations. The only observed reproductive efforts within the 3 areas took place within these complex systems.

Density and diversity of plant growth had no measurable direct effect on the number or types of burrows. Evidence indicated that less complicated burrow types were concentrated within areas of high plant species diversity and complex burrow systems were located in areas characterized by low plant species diversity.

Significant correlations existed among many internal and external dimensional attributes, and the physiographic and edaphic features of the environment. Number, type and distance between within system openings, number and type of tunnels, number of chambers and penetration of the bank by the burrow systems were all positively associated with each other and with low bank slopes and loam soils.

Readily detectable structures and physical features defining muskrat burrow types, in combination with sign census and a capture-recapture program could be used to qualify the habitat's suitability for muskrats and to quantify burrowing muskrat populations.

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Appendix 1. Significant Correlation Coefficients Among Burrow Variables.

CORRELATION COEFFICIENTS / PROB > |R| UNDER H0:RHO=0 / N = 85

MAREA

MAREA	STYP	CNOSPEC	HOP	CAGRAMI	CACOMPO	WCHMB	CAALISM	CACAESA	WOP	CAURTIC
1.00000	0.74440	-0.48619	0.43202	-0.39546	-0.39407	0.35387	-0.35190	0.34251	0.33630	-0.25422
0.0000	0.0001	0.0001	0.0001	0.0002	0.0002	0.0009	0.0010	0.0013	0.0017	0.0189

STYP

STYP	MAREA	CAALISM	WOP	WCHMB	HOP	CACAESA	LT	CAGRAMI	CNOSPEC	SSLOP	CACHENO
1.00000	0.74440	-0.47476	0.36653	0.31743	0.31741	0.31421	-0.30536	-0.29121	-0.28483	0.24907	0.21741
0.0000	0.0001	0.0001	0.0006	0.0031	0.0031	0.0034	0.0045	0.0069	0.0082	0.0215	0.0456

BSLOP

BSLOP	CHTW	SSLOP	CATREES
1.00000	0.80101	0.45924	-0.23095
0.0000	0.0001	0.0001	0.0335

SSLOP

SSLOP	PEN	BSLOP	LT	DWS	WT	CHTW	NT	OVBRDN	NOBS	NOP	NCHMB	TT	CATREES
1.00000	-0.47585	0.45924	-0.45314	-0.38984	-0.36025	0.33531	-0.32247	0.31863	-0.31666	-0.31114	-0.30776	-0.29374	-0.27103
0.0000	0.0001	0.0001	0.0001	0.0002	0.0007	0.0017	0.0026	0.0030	0.0032	0.0038	0.0042	0.0064	0.0121

NOP

NOP	NOBS	NT	NCHMB	TT	PEN	LT	TOP	DWS	CHTW	DNEXTB	SSLOP	WT	CAPOLYG
1.00000	0.94254	0.93434	0.91219	0.78613	0.76831	0.71760	0.66894	0.60903	0.41695	0.33713	-0.31114	0.28042	0.25807
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0016	0.0038	0.0093	0.0171

WOP

WOP	CAALISM	HOP	STYP	MAREA	LT	CACOMPO	WT
1.00000	-0.47236	0.37037	0.36653	0.33630	-0.31806	0.29085	-0.23371
0.0000	0.0001	0.0005	0.0006	0.0017	0.0030	0.0069	0.0313

HOP

HOP	MAREA	WOP	OVBRDN	STYP	CHTW	CAALISM
1.00000	0.43202	0.37037	0.32165	0.31741	-0.24166	-0.22243
0.0000	0.0001	0.0005	0.0027	0.0031	0.0259	0.0408

TOP

TOP	NOP	TT	DWS	NOBS	NT	LT	NCHMB	PEN	CAPOLYG	CATREES	SSLOP	WT	CHTW
1.00000	0.66894	0.64911	0.63909	0.52833	0.48912	0.48535	0.46301	0.42667	0.29881	0.25746	-0.24644	0.24319	0.22935
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0055	0.0174	0.0230	0.0249	0.0347

DWS

DWS	TT	TOP	LT	NOP	NOBS	NT	NCHMB	PEN	WT	SSLOP	CACOMPO
1.00000	0.68240	0.63909	0.61376	0.60903	0.56660	0.54885	0.52897	0.48801	0.39782	-0.38984	-0.23703
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002	0.0002	0.0289

DNEXTB

DNEXTB	PEN	NOP	CHTW	TT	NT	NCHMB	NOBS	CNOSPEC
1.00000	0.36966	0.33713	0.31473	0.31270	0.26567	0.25681	0.25523	-0.22082
0.0000	0.0005	0.0016	0.0034	0.0036	0.0140	0.0177	0.0184	0.0423

Appendix 1--Continued.

NT

NT	NOBS	NCHMB	NOP	PEN	TT	LT	DWS	TOP	CHTW	WT	SSLOP	DNEXTB
1.00000	0.98151	0.97405	0.93434	0.81333	0.75862	0.74293	0.54885	0.48912	0.36976	0.32584	-0.32247	0.26567
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0005	0.0023	0.0026	0.0140

WT

WT	LT	PEN	DWS	SSLOP	NT	TT	NOP	NOBS	TOP	NCHMB	WOP
1.00000	0.56285	0.44326	0.39782	-0.36025	0.32584	0.32320	0.28042	0.26438	0.24319	0.24210	-0.23371
0.0000	0.0001	0.0001	0.0002	0.0007	0.0023	0.0026	0.0093	0.0145	0.0249	0.0256	0.0313

LT

LT	PEN	NT	NOP	NOBS	NCHMB	TT	DWS	WT	TOP	SSLOP	WOP	STYP
1.00000	0.82786	0.74293	0.71760	0.69594	0.66975	0.63320	0.61376	0.56285	0.48535	-0.45314	-0.31806	-0.30536
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0030	0.0045

TT

TT	NOP	NT	NOBS	PEN	NCHMB	DWS	TOP	LT	WT	DNEXTB	SSLOP	CHTW	CAPOLYG
1.00000	0.78613	0.75862	0.72372	0.68941	0.68606	0.68240	0.64911	0.63320	0.32320	0.31270	-0.29374	0.26420	0.21992
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0026	0.0036	0.0064	0.0146	0.0431

CACOMPO
-0.21585
0.0472

NCHMB

NCHMB	NOBS	NT	NOP	PEN	TT	LT	DWS	TOP	CHTW	SSLOP	DNEXTB	WT
1.00000	0.99218	0.97405	0.91219	0.78225	0.68606	0.66975	0.52897	0.46301	0.38133	-0.30776	0.25681	0.24210
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0003	0.0042	0.0177	0.0256

WCHMB

WCHMB	LCHMB	MAREA	STYP	CACAESA	CANAJAD	CACOMPO
1.00000	0.37653	0.35387	0.31743	0.31319	-0.22256	-0.21684
0.0000	0.0004	0.0009	0.0031	0.0035	0.0406	0.0462

LCHMB

LCHMB	WCHMB	CACOMPO
1.00000	0.37653	-0.23395
0.0000	0.0004	0.0312

PEN

PEN	LT	NT	NOBS	NCHMB	NOP	TT
1.00000	0.82786	0.81333	0.78294	0.78225	0.76831	0.68941
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

OVBRON

OVBRON	HOP	SSLOP	CACAESA
1.00000	0.32165	0.31863	0.28330
0.0000	0.0027	0.0030	0.0086

Appendix 1--Continued.

CHTW

CHTW	BSLOP	NOP	NOBS	NCHMB	NT	PEN	SSLOP	DNEXTB	CATREES	TT	HOP	TOP
1.00000	0.80101	0.41695	0.38331	0.38133	0.36976	0.34074	0.33531	0.31473	-0.29402	0.26420	-0.24166	0.22935
0.0000	0.0001	0.0001	0.0003	0.0003	0.0005	0.0014	0.0017	0.0034	0.0063	0.0146	0.0259	0.0347

NOBS

NOBS	NCHMB	NT	NOP	PEN	TT	LT	DWS	TOP	CHTW	SSLOP	WT	DNEXTB
1.00000	0.99218	0.98151	0.94254	0.78294	0.72372	0.69594	0.56660	0.52833	0.38331	-0.31666	0.26438	0.25523
0.0000	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0003	0.0032	0.0145	0.0184

CAACANT

CAACANT	CACHENO	CAALISM	LT	WT	DNEXTB
1.00000	0.24254	-0.12108	0.10138	0.09556	0.09505
0.0000	0.0253	0.2697	0.3559	0.3843	0.3869

CAALISM

CAALISM	STYP	WOP	CACOMPO	MAREA	CATREES	HOP
1.00000	-0.47476	-0.47236	-0.35204	-0.35190	0.23689	-0.22243
0.0000	0.0001	0.0001	0.0010	0.0010	0.0290	0.0408

CACAESA

CACAESA	MAREA	STYP	WCHMB	DVBRDN	CAGRAMI
1.00000	0.34251	0.31421	0.31319	0.28330	-0.22641
0.0000	0.0013	0.0034	0.0035	0.0086	0.0372

CACHENO

CACHENO	CAACANT	CAGRAMI	STYP
1.00000	0.24254	0.22957	0.21741
0.0000	0.0253	0.0346	0.0456

CACOMPO

CACOMPO	MAREA	CNOSPEC	CAALISM	WOP	DWS	LCHMB	WCHMB	TOP	TT
1.00000	-0.39407	0.37172	-0.35204	0.29085	-0.23703	-0.23395	-0.21684	-0.21658	-0.21585
0.0000	0.0002	0.0005	0.0010	0.0069	0.0289	0.0312	0.0462	0.0465	0.0472

CAGRAMI

CAGRAMI	CNOSPEC	MAREA	STYP	CACHENO	CACAESA
1.00000	0.53260	-0.39546	-0.29121	0.22957	-0.22641
0.0000	0.0001	0.0002	0.0069	0.0346	0.0372

CALABIA

CALABIA	CNOSPEC
1.00000	0.38123
0.0000	0.0003

CANAJAD

CANAJAD	CNOSPEC	WCHMB
1.00000	0.25670	-0.22256
0.0000	0.0177	0.0406

Appendix 1--Continued.

CAPOLYG

CAPOLYG	TOP	NOP	TT
1.00000	0.29881	0.25807	0.21992
0.0000	0.0055	0.0171	0.0431

CATREES

CATREES	CHTW	SSLOP	TOP	CAALISM	BSLOP
1.00000	-0.29402	-0.27103	0.25746	0.23689	-0.23095
0.0000	0.0063	0.0121	0.0174	0.0290	0.0335

CAURTIC

CAURTIC	MAREA
1.00000	-0.25422
0.0000	0.0189

CNOSPEC

CNOSPEC	CAGRAMI	MAREA	CALABIA	CACOMPO	STYP	CANAJAD	DNEXTB
1.00000	0.53260	-0.48619	0.38123	0.37172	-0.28483	0.25670	-0.22082
0.0000	0.0001	0.0001	0.0003	0.0005	0.0082	0.0177	0.0423

Appendix 2

Live Trapping

Between 3 October 1976 and 8 August 1977, 45 trap nights were spent attempting to live trap, burrow dwelling muskrats within the Research Area. Because of the low level of success (8 captures in 45 trap sets), the original objectives of this trapping campaign were not successfully completed.

Trapping began with the placement of the prototype live trap in an active burrow 90 m from the western end of the southern bank in Study Area 1. One square end of the lower section was placed just at the opening of the burrow in 25 cm of water. A V-shaped guiding fence was placed so that the stream side end of the bottom section was located at the apex of the V. This set was in place from 2100 3 October until 0700 4 October 1976. During this time 2 adults, 2 subadults and 1 young muskrat were captured. The adults had claimed and defended the upper section of the trap. As either the subadults or young muskrat approached the upper drop door 1 of the adults would rush the intruder and force them back into the center section. Lack of equipment at this time precluded tagging and measuring of the captured animals. Muskrats were released at the burrow opening. The adults swam immediately to deep water and submerged. The subadults and kit, after some hesitation, reentered the burrow.

Unsuccessful sets were made on the south bank of Study Area 2 at burrows 39, 41, 46 and on 12 November 1976 and burrows 48, 58 and 59 on 13 November 1976. On 10 December 1976 an unsuccessful trap set was placed in the same burrow in Study Area 1 in which the prototype was tested. On 17 March 1977 a second unsuccessful set was made in a burrow 5 m west on the south bank.

Two sets were made in a pond adjoining the north bank of the south fork of the lake. One trap was placed in the center of a channel 1 m wide and 30 cm deep connecting the pond to the main body of the south fork. Guiding fences were constructed from 1-2 cm branches on both ends of the trap. A second trap was placed in a burrow in a dike separating the pond from a goose rearing pen to the west. The latter set was prompted by the sighting of an adult muskrat within 1 m of the burrow opening. As the trap was being placed the muskrat swam from the burrow, continued swimming south, left the pond and crossed a peninsula separating the pond from the south fork of the lake. After placing the trap in the burrow opening, a guiding fence was constructed on the opposite end. The burrow opening was half submerged and showed claw marks from recent digging efforts.

Between 1900 CST 25 March and 0800 CST 26 March a large female was captured. During all portions of the handling procedure the female showed little evidence of fear. At 1 point, when suspended by the tail for total length measurements, she began urinating in spurts. This continued until her tail was released. Small chips on the lower margin of her upper incisor and bloody gums indicated that she may have gnawed on the metal in the upper holding cage of the trap.

After measuring and ear tagging the muskrat was released within 2 m of the point of capture. After approximately 15 seconds of hesitation she swam to and reentered the burrow at which she was captured.

On 30 March 2 traps were placed in 2 burrows 200 m east of the site at which muskrat number 1 was captured. On 9 May, 2 traps were placed in 2 openings of burrow 32 in Study Area 2. A large number of tracks in the vicinity of the trap set indicated that a large coyote had visited the area during the night of 9 May or the morning of 10 May; these sets were unsuccessful.

On 10 May 1 of the 2 traps in burrow 32 was placed in an opening 50 cm beneath the water in burrow 30. The remaining trap was left in place. On 11 May and 12 May the traps were shifted to different under openings of burrow system 32. Several drops of musk lure were placed on the traps just above the water line. The openings trapped on 10 May were fenced with sticks.

During the night of 12 May or morning of 13 May a small male, muskrat number 2, was captured in the center under water opening of burrow number 32. This muskrat was extremely agitated from the moment of my approach to the trap to the instant of release. When in the handling cage he urinated profusely and constantly bit and clawed the moveable restraining lid. During this period he lost both upper incisors below the gum lines and severely damaged both lower incisors. The base of his claws were bleeding by the time of release from the handling cage. Upon release, muskrat number 2 immediately reentered the burrow opening at which he was captured.

Unsuccessful trap sets were made during May and June in 2 burrows on the south bank opposite from burrows 1 and 4. Other unsuccessful sets were made during this period in burrows 28, 21, 22, in a burrow complex at the north end of the dike in which muskrat number 1 was captured and in a burrow system on the north bank upstream from Study Area 2.

On 8 August a trap was placed in opening number 2 of burrow 30.

This area showed much evidence of feeding on dryland stands of ragweed and sunflowers by muskrats. During the night of 8 August or the early morning of 9 August a juvenile male was captured. This capture, muskrat number 3, was extremely agitated when confined within both the trap and the handling cage. During confinement this small male lost the lower third of both upper incisors. When suspended by the tail and grasped just behind the shoulder he became docile. Upon release muskrat number 3 entered an opening 1 m east of the point of capture.

Appendix 3

Beaver, Raccoon and Mink Activity Patterns

During 8 September 1976 to 13 November 1977, beaver, raccoon and mink activities were observed and recorded throughout the research area. Special emphasis was placed on the observation of the activities of these animals in or about the 3 study areas (Figs. 8, 9, 10).

During September 1976 beaver sign consisting of an occasional track and some desultory cutting of 6 to 10 cm cottonwood, willow and ash saplings occurred in the 3 study areas. Actual sightings of beaver occurred in Study Area 1 and the upstream half of Study Area 2, usually during late afternoon to early evening hours.

From October through November 1976 the level of feeding activity increased in Study Area 1 and ceased in Study Area 2. Over 100 green ash 6 to 50 cm d.b.h. were harvested on both banks of Study Area 1. A limited amount of cutting occurred in the adjacent end of Study Area 3. Much of this material was incorporated into a lodge 8 m in diameter, on the downstream end of the south bank. The remainder was used to resupply 2 food caches located in the water just east of the lodge and 2 additional food caches 125 m west in the old creek channel. Food caches in the inundated stream channel apparently supplied the beaver utilizing the 2 adjacent active burrows in the south bank and the 3 in the north bank.

During December 1976, 4 under ice beaver sightings were made at the lodge and 3 of the burrows on the southern bank of the study area. On 11 December 1976 an apparently healthy young beaver was temporarily cornered on the ice and closely approached. From 14 December 1976 to 6 July 1976 no beaver activity was detectable in Study Areas 1 and 3.

On 7 July 1977 during an inspection of muskrat and beaver burrows in Study Area 1, 2 partial beaver skeletons and a well rotted 10 X 15 cm section of beaver skin was found in 2 of the formerly active burrows in the north bank. This finding prompted a close inspection of beaver burrows in the north bank and lodge on the downstream end of the south bank. All lacked signs of any recent activity and the western most burrow had collapsed. During 14 December to 6 July only 1 sighting of a living beaver was sighted in its burrow on the north shore of the north creek channel 150 m upstream from the western most boundary of Study Area 2.

From 8 September 1976 to 6 July 1977, beaver activity was regularly observed on the south fork of the lake and in the bay near the northeast end of the dam. These indicators of activity included tree cuttings, tracks and maintenance on 2 small dams in the south stream channel.

Observations of raccoon and mink activity patterns from 8 September 1976 to November 1977 consisted of infield gross scat examination and location and monitoring of active dens.

Detectable raccoon activity occurred in the 3 study areas during fall of 1976 and spring, summer and fall of 1977. A large occupied den located beneath a large slash pile on the western end of the southern bank of Study Area 1 was the locus of most activity in both Study Areas 1 and 3. Heavily traveled trails led overland and along the shorelines to the south, west and east. In Study Area 2, movements up and downstream along a trail near the water line on the south bank was the predominant indicator of raccoon activity.

Field examination of scats during fall of 1976 and 1977 suggested that the diet of the resident raccoons consisted of a combination of local wild fruits and fish. Summer diets of raccoons in Study Areas 1 and 3 were primarily composed of fish and crayfish and diets of raccoons in Study Area 2 consisted of fish and corn from a nearby food plot.

From late January 1977 to the end of March 1977 atypical feeding behavior (Wilson 1953) was observed in Study Areas 1 and 2. Approximately 15 burrows were dug into by raccoons. Shortly after the initiation of this digging, muskrat underfur, guard hairs and bones became a recognizable constituent of most raccoon scats located in Study Areas 1, 2 and 3. April scat checks indicated a return to fish and unidentifiable plant material.

One den in Study Area 1 and 2 centers of mink activity in Study Area 2 were monitored from November 1976 through August 1977. The centers of activity were traced to 2 dens contained within 2 separate muskrat burrow systems in Study Area 2 during the first week in August 1977.

Mink tracks were observed throughout the study areas from September 1976 to November 1977. Mink scats, although few in number, were encountered frequently enough to provide some indication of changes in diets. The majority of mink scats included fish bones and scales throughout the recording period. Muskrat underfur and guard hairs were an uncommon but detectable content of mink scats. The 1 exception to this occurred during January through March of 1977. The majority of scats located during this period contained large quantities of muskrat hair and bones. As with raccoon scats, mink scats indicated a return to the normal diet during April.

Appendix 4. Descriptive statistical values for burrow variables.

Variable	All Burrows[1] (Individual Structures)[2] Mean	Min	Max	SD
STYP	1.494	1	3	0.781
BSLOP	2.294	-72.1 (-90.0)	45.0 (65.1)[a]	20.590
SSLOP	36.242	0.1	79.6	18.131
NOP	1.563	1	14	1.886
WOP	0.235	0.075 (0.070)	0.600 (0.720)[b]	0.137
HOP	0.127	0.070 (0.060)	0.243 (0.255)[c]	0.037
TOP	1.118	1	2	0.324
DWS	0.094	0	0.879 (1.630)[d]	0.208
DNEXTB	3.976	0	43.286 (44.92)[e]	7.273
NT	1.153	0	29	3.490
WT	0.077	0 (0.090)	0.580 (0.79)[f]	0.095
LT	0.264	0 (0.117)	2.113 (11.250)[g]	0.382
TT	1.153	1	3	0.423
NCHMB	1.953	0	34	3.945
WCHMB	0.194	0 (0.080)	0.550	0.101
LCHMB	0.216	0 (0.080)	0.620	0.100
PEN	0.502	0	2.566 (6.150)[h]	0.367
OVBRDN	0.283	0.040	2.600	0.344
CHTW	0.012	-0.790	0.750	0.217
NOBS	2.129	1	34	3.942
CAACANT	0.071	0	4	0.457
CAALISM	1.094	0	5	1.411
CACAESA	0.400	0	8	1.513
CACHENO	0.141	0	11	1.197
CACOMPO	0.765	0	4	1.297
CAGRAMI	15.976	0	95	17.691
CALABIA	0.071	0	1	0.257
CANAJAD	0.094	0	2	0.366
CAPOLYG	0.011	0	1	0.108
CAROSAC	0,047	0	1	0.213
CATREES	0.094	0	1	0.294
CAURTIC	0.271	0	8	1.285
CNOSPEC	4.906	1	10	2.250

1 One observation per burrow (N=85)

2 All observations.

a N=116 b N=133 c N=121 d N=167 e N=133 f N=99 g N=99 h N=164